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MALACOLOGIA

International Journal of Malacology

ol. 54(1–2)

2011

MALACOLOGIA
http://malacologia.fmnh.org

One of the World's Leading Malacological Journals
Journal Impact Factor 1.024 (2010)

Founded in 1961

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P.O. Box 385
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MALACOLOGIA, 2011, 54(1–2): 1–76

THE PUBLICATIONS AND MALACOLOGICAL TAXA OF WILLIAM WOOD (1774–1857)

Eugene V. Coan[I]* & Richard E. Petit[II]

ABSTRACT

William Wood (1774–1857), trained as a physician, soon turned his attention to natural history book publication and sales. Working in London, his chief malacological publications were the *General conchology* (1814–1815; reprinted in 1835), two editions of the *Index testaceologicus* (1818, 1823–1825; the latter reprinted in 1828), and a *Supplement* (1828) to the *Index* containing many new species. He made available 282 specific names, of which 109 are now considered valid. Type lots of many of his species are present in The Natural History Museum, London, some newly located during the present study.

Key words: William Wood, John Edward Gray, taxonomy, biography, bibliography.

INTRODUCTION

The purpose of this paper is to provide a biography, a complete bibiliography, and list of taxa of the early British malacologist William Wood. We have relied on published sources, examination of several copies of his major works, assistance of a biographical researcher in England, and a two-week search by one of us (EVC) for unrecognized type material in The Natural History Museum, London. In our treatment, we use these abbreviations: NHMUK, the collections of The Natural History Museum, London, U.K. [shown in Wood's works as "Br.M."]; ICZN, the International Commission on Zoological Nomenclature.

BIOGRAPHY

William Wood (22 Feb. 1774–28 May 1857) was born in Kendal, a market town in northwestern England about 360 km north-northwest of London. He was baptized on March 16 in the parish of Lowther. The son of John and Frances Wood, nothing is known about his early life. He studied medicine at St. Bartholomew's Hospital in London under John Abernethy (1763–1831), who was noted for an interest in the effect of vegetarianism on disease. Wood then began medical practice at Wingham, about 10 km east of Canterbury.

While in Wingham, Wood married Juliana Whitfield (24 May 1772–27 April 1839) on 30 November 1797[1]. Mary Halsnod Wood (1798–1874), the eldest child of William and Juliana Wood, was born on 23 December 1798. Their son George was born on 29 October 1800, and William, Jr., on 5 September 1803.

By this time, William's interests increasingly turned to natural history, and he traveled to London to attend meetings of the Linnean Society[2]. He was elected a Fellow of that society on March 20, 1798, the proposers noting his natural history studies. His first work and only paper was on the hinges of bivalves, read to the Linnean Society on January 6, 1801, and published the following year (Wood, 1802). This was the first detailed treatment of the subject, the hinge teeth being indicated by letters defined on the plate explanation. He introduced one new species, *Mactra alba*, now *Abra alba* (W. Wood, 1802). The figures

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[1] Name rendered as Julianna on some census and probate forms and in some genealogical records as "Elizabeth Juliana". This last this is the result of error, as she is referred to in her mother's will simply as Juliana Wood, and her sister was referred to as Elizabeth Shaw in that will. Her sister, Elizabeth Hester Whitfield, married a cousin, the noted architect John Shaw.

[2] The inconsistent spellings "Linnaean" and "Linnean" arise from the selective use of the name of the founder of the system of nomenclature, Linnaeus or von Linné. The spelling "Linnean" was in common use in England in Wood's time, as shown by the naming of the Linnean Society. In citing others, their usage is maintained. In our own statements, "Linnaean" is used.

[I] Research Associate, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 94105-2936, U.S.A.
[II] 806 St. Charles Road, North Myrtle Beach, South Carolina 29582-2846, U.S.A.
*Corresponding author: genecoan@gmail.com

in this article were prepared by Henry Boys (1775–1868), son of the malacologist William Boys (1735–1803), whose collection Wood acknowledged[3] (Fig. 1).

In about 1803, Wood moved to London, his first address being on North Audley Street, number unknown, just west of Hyde Park (Davis, 2004).

In 1807, William Wood produced a three-volume natural history, *Zoography; or, the beauties of nature displayed*, with illustrations by William Daniell (1769–1836), father of Rose and Emma Daniell, who are discussed below. The first volume was devoted to mammals and birds, the second to an array of other vertebrates and invertebrates, and the last to plants. The only mollusks treated, in volume 2, were the bivalve genera *Pholas* and *Solen*, and the cephalopod genus *Argonauta*.

The Preface to *Zoography* is signed W. Wood, Titchfield Street, Nov. 1807. This is now Great Titchfield St., number unknown, a few blocks northeast of his North Audley street address. Elizabeth Whitfield, Juliana's mother, was living with the Woods at Titchfield St., London, when she died in 1812.

He was elected a Fellow of the Royal Society in 1812, no doubt influenced by his publication that year of a 20-volume updated edition of Smellie's translation of Buffon's Natural History (Wood, 1812), illustrated with 680 plates and almost 10,000 pages covering geography, mammals, and birds. Smellie's translation, which had gone through three editions, was a mere nine volumes (Smellie, 1780–1781, 1785, 1791). The first ten volumes of Wood's version of Buffon were printed by a Charles Wood of 13 Pippin's Court, London, but he appears to be no relation.

It comes as little surprise that by 1814, at the age of 40, he had abandoned medicine and taken up the profession of bookseller and publisher. Over the next two years, Wood produced his first significant malacological book, *General conchology*, its Advertisement (p. iv) indicating the Tichfield St. address. The *General conchology* was intended to be the first of two or more volumes on mollusks, but the project was superceded by his *Index testaceologicus*, which was less expensive to produce.

By 1816, Wood moved his publications business to 428 The Strand[4], in London's Covent Garden district, home of many book publishers and dealers. He seems to have become a partner with Richard Floyer, who had run the firm from 1805 until then. The firm is listed in city directories as Floyer & Wood from 1816 to 1817, then as Wood & Floyer from 1817 to 1819. By 1819, the firm was in William Wood's name alone[5].

The next Wood work to appear was his *Index testaceologicus* (1818). His goal with the *Index* was to list previously named mollusks, with citations to published figures, and only one or two images for each genus by Wood himself were provided. No descriptions were included.

His next production was a two-volume *Illustrations of the Linnaean genera of insects* (Wood, 1821).

In 1823, Wood issued the first part of a second edition of his *Index testaceologicus*, completed by a second part two years later (Wood, 1823–1825). This was the first post-Linnaean binominal effort to offer illustrations of almost all of the known species of mollusks. A second printing, differing in minor details from the original, appeared in 1828 (Wood, 1828a), along with the far more important *Supplement* (Wood, 1828b), which is discussed in detail below.

In the meanwhile, because he also sold natural history books, he produced a sales catalogue organized by taxonomic group (Wood, 1824). A much enlarged version of this catalogue appeared eight years later (Wood, 1832). Each contained the same plate of mollusks, without captions, lifted from his (1823–1825) *Index*, the 1832 version having additional natural history plates. According to Swainson (1840: 380), he was "the most learned bookseller in London for works connected with natural history". Among the works produced by Wood's firm was the first edition of Swainson's *Exotic conchology* (Swainson, 1821–1822) and his *The naturalist's guide* (1822).

In 1829, Wood published a 34-page pamphlet that organized the species of the *Index* and *Supplement* in plate and figure sequence (Wood, 1829a), with the Lamarckian genera indicated for each (Reynell, 1919).

His next work, issued that same year (Wood, 1829b), was a reprint of the plates from

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[3] The Boys collection was acquired by George Montagu (1753–1815), but none of his material has been recognized in the British Museum (Natural History) or the Exeter Museum where parts of the the Montagu collection now reside (Dance, 1986: 206, 219).

[4] This building has since been replaced by another, more modern one.

[5] Not to be confused with a prolific New York City publisher of the same name who specialized in medical text books.

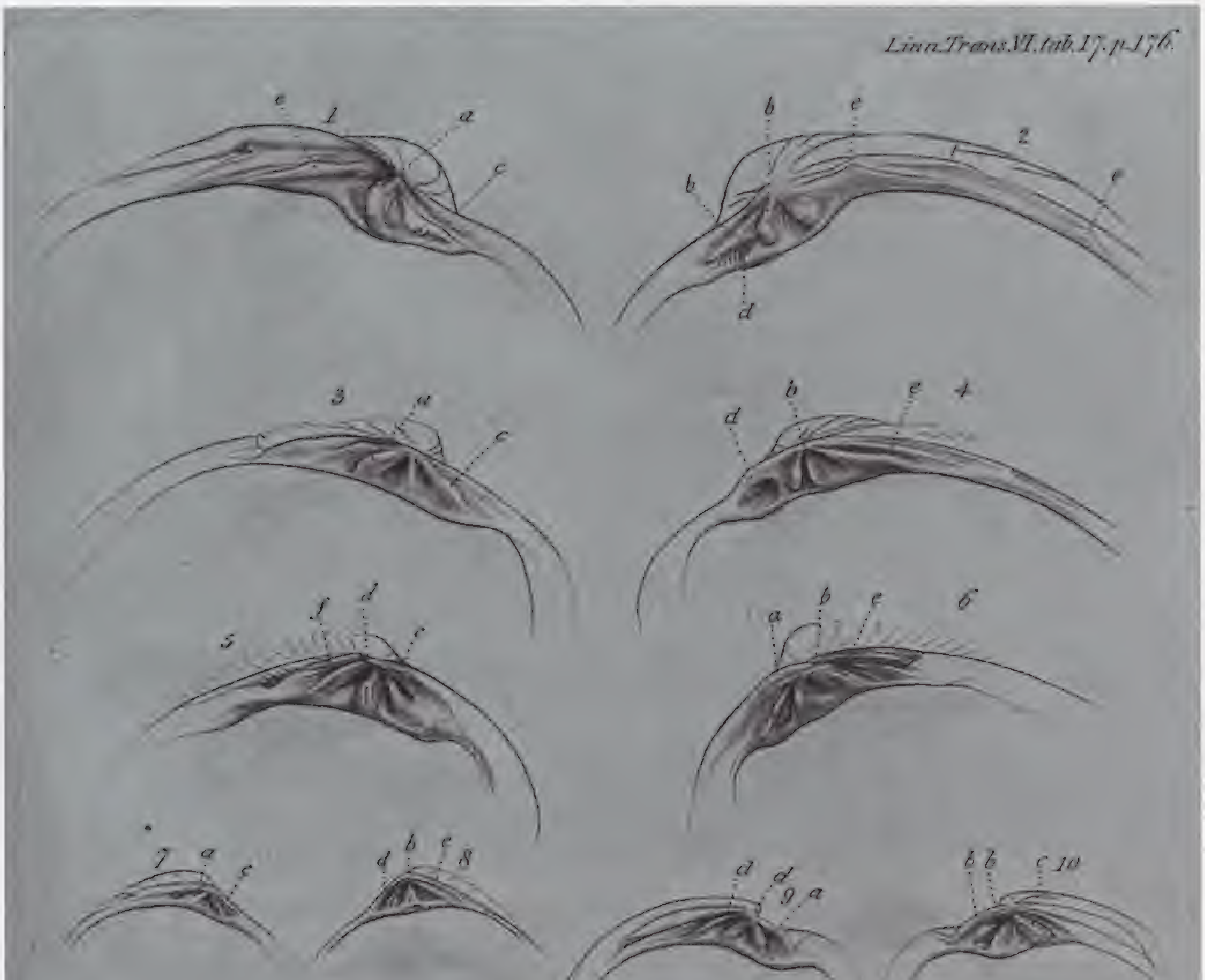

FIG. 1. Plate 17 from Wood (1802) showing hinge features of eight bivalve species.

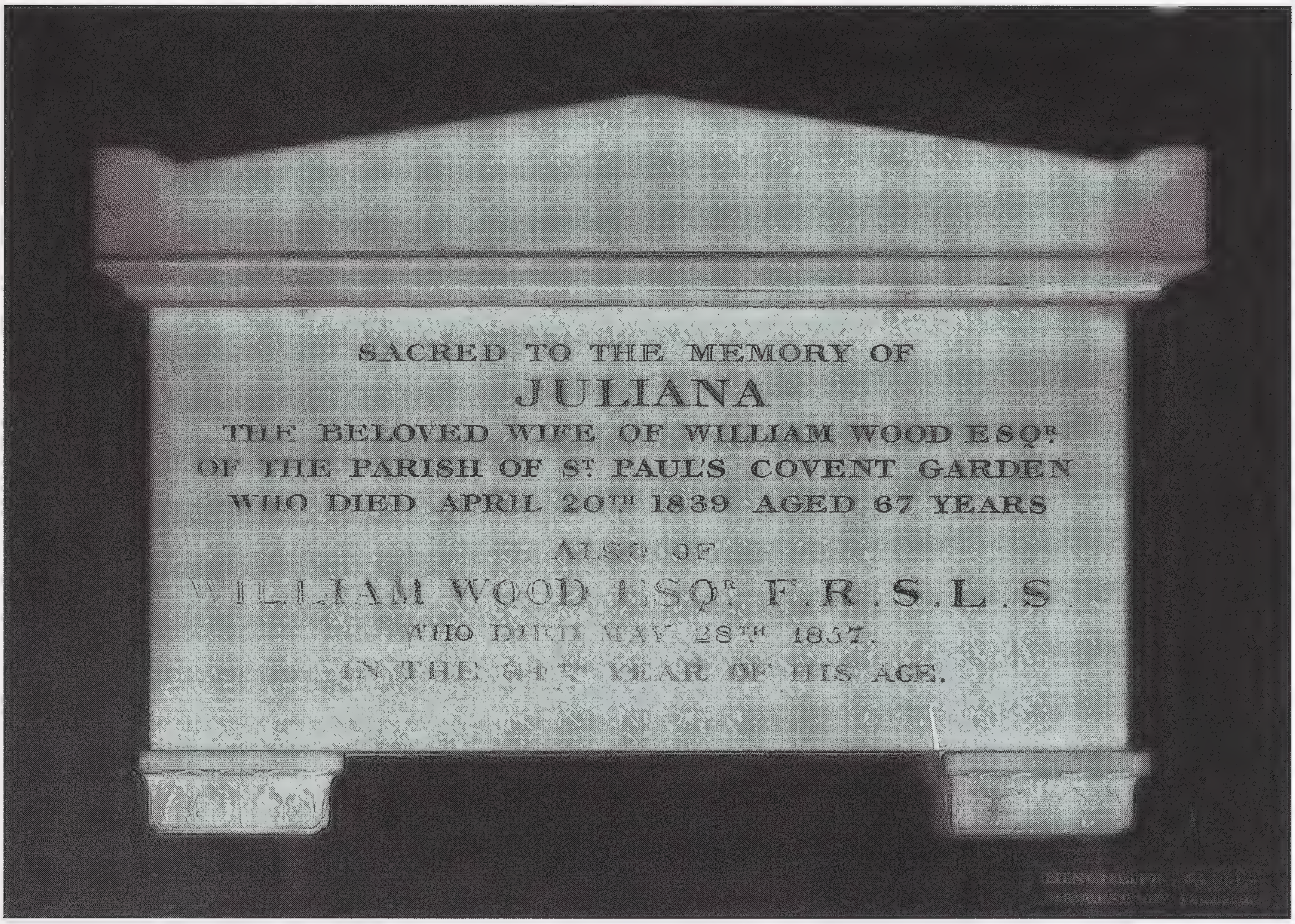
SACRED TO THE MEMORY OF
JULIANA
THE BELOVED WIFE OF WILLIAM WOOD ESQR
OF THE PARISH OF ST PAUL'S COVENT GARDEN
WHO DIED APRIL 20TH 1839 AGED 67 YEARS
ALSO OF
WILLIAM WOOD ESQR F.R.S.L.S.
WHO DIED MAY 28TH 1857.
IN THE 84TH YEAR OF HIS AGE.

FIG. 2. Memorial plaque to Juliana and William Wood, St. Martin's, Ruislip, England.

Brander's *Fossilia Hantoniensia* (Brander, 1766), providing supplemental references from Lamarck's works and from James and James de Carle Sowerby's *Mineral conchology of Great Britain* (1812–1846). Apart from the 1835 reprint of *General conchology*, this was Wood's last malacological publication[6].

In 1832, Wood's business had relocated to 39 Tavistock St.[7] in Covent Garden, two blocks northeast of his prior address on The Strand.

From 1833 to 1838, Wood published the *Index entomologicus* in 22 parts. When completed, it was reissued in 1839 (Griffin, 1931). John Obadiah Westwood (1805–1893) oversaw a second edition, with his own supplement, after Wood's retirement (Wood & Westwood, 1854).

In early 1839, Wood turned the business over to William Wood, Jr., who remained on Tavistock St. until at least 1855, and William Wood, Sr., and Juliana retired to the town of Ruislip (pronounced "rice-lip"), 23 km northwest of central London, where their daughter and her family lived. Wood's final work was the start of an illustrated book on the fishes of Great Britain (Wood, 1842–1843), but only three of 13 intended parts were issued.

Ruislip was then a small but ancient rural village. Unfortunately, Juliana Wood died in Ruislip on 27 April 1839, shortly after they moved there. William Wood continued living in Ruislip, where he died on 28 May 1857 and was buried on 2 June 1857. Juliana was memoralized on a St. Martin's wall plaque onto which William was later added (Fig. 2).

The statements by Anonymous (1859) and by Davis (2004) that when William Wood died that he left one son is incomplete, because, as was mentioned above, he was survived by two sons and a daughter. The genealogical picture is a little confusing, and we hope readers will not object to a few additional paragraphs about this family to clarify matters.

The Wood's daughter, Mary Halsnod Wood, married Christopher Packe on 15 November

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[6] All of Wood's malacological works are now available online.

[7] This building still stands, and Wood's office seems now to be a coffee shop.

1821. Rev. Christopher Packe (1792–1878) was Vicar at St. Martin's, Ruislip, from 1834 to 1878. In applying for the Vicarage there, he wrote that he hoped "the air of the country" would be beneficial for his children, as by 1834, when they moved there, they had lost five of their nine children. After the move to Ruislip they had an additional five children, one of whom died at age 3, but the others survived childhood. It is known that one, Rosa [not to be confused with Rose Wood], was born in 1835, lived until 1934.

As noted above, William and Juliana had two sons, George (29 October 1800–26 March 1877) and William (5 September 1803–5 September 1865). In order to properly account for them we must first introduce the Daniell family.

The Wood family is entwined with that of the noted artist William Daniell (1769–1837), who illustrated Wood's 1807 *Zoography*. He had four daughters, three of whom enter into our narrative. Here, it is necessary to give the solution to a problem that we found vexing until resolved. John George Wood (1812/13–?), married Rose Daniell (1811–31 December 1913) on 17 September 1834, but he was not the son of William and Julianna, although it is possible that he may have been distantly related[8]. Rose's second husband was George Wood, elder son of William Wood, Sr.

William's son George Wood (29 October 1800–26 March 1877) had gone to India, where he held a position as a Judge with the East India Company. He married three times there, having nine children by his first wife. He returned from India, a widower, sometime before 30 March 1864, when he married Rose Wood. They lived in Chertsey, about 29 km southwest of central London, where George's brother William lived with his wife Emma, Rose's sister.

William Wood, Jr. (5 September 1803–5 September 1865) was the youngest of the three Wood siblings. William did most of the illustrations for the *Index Testaceologicus* and its *Supplement*. He married Emma Daniell on 3 September 1840. Emma was the second daughter of William Daniell and an older sister of Rose Daniell Wood. William took over the book business upon his father's retirement. Between 1855 and 1861, William and Emma retired to Chertsey, where the census lists his occupation as artist. They did not have children, and Emma bequeathed her entire estate to her younger sister, Marianne Charlotte Daniell[9].

No images of either William Wood, Sr. or Jr., have come to our attention.

Wood is a very common surname, and several naturalists with that name published new zoological taxa at the same time as William Wood. His family has no relationship with that of Charles Thorold Wood (1777–1852) and his son Neville Wood (fl. 1835–1839), both of whom published on birds in the 1830s. The William W. Wood of New England who described new species of fish in the 1820s also seems to be of no relation. In malacology, Searles Valentine Wood (1798–1880) published an extensive monograph on Neogene mollusks (1848–1882), with the third supplement (1882) edited by his son, Searles Valentine Wood, Jr. (1830–1884), after his death (Petit & Boss, 1989). Because both S. V. Wood and W. Wood each authored many molluscan species, it is recommended that their initials be used in referring to their taxa. Finally, the naturalist John George Wood (1827–1889), who published many field guides, including The *Common shells of the sea-shore* in 1865, is not to be confused with John George Wood, the first husband of Rose Daniel, and neither was, to our knowledge, a blood relative of William Wood.

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[8] On their marriage license and certificate, John George Wood is listed as "Bachelor", and Rose as "Spinster". In his will, William Daniell listed his daughters and made specific provisions for three of them. He then wrote: "As to my third daughter Rose Wood is provided with a good husband ... [portion illegible] ... and to her husband George Wood my silver snuff box." Between 13 April 1837, when the will was first written, and 1 May 1837, the quoted sentence was struck over and emended so that Rose's inheritance was exactly that of the other two daughters. What happened to John George Wood is not known, but it is probable that he died while they were resident in some other country, as no death record has been located in England.

[9] We have endeavored to obtain additional biographical information about this family. In addition to the problems normally encountered in attempting to obtain, at long distance, data that is 200 years old and may not still exist, our situation was made difficult by the prevalence of the family name Wood and the popularity of such names as William, John, and George. It is hoped that someone in England will follow up on the information we have, as unraveling some of it should be interesting as well as informative. The rather large amount of data we amassed in this process, extending to other family members and even other associated families, is now held at the Santa Barbara Museum of Natural History. It consists of marriage, baptism, and burial certificates, as well as census reports and other documents. Some of the children of George Wood married in India and emigrated from there to Canada and Australia. The Wood family was highly respected. At least one of George's sons was an official in the British India Company. The marriage certificate of George and Rose in 1864, which requires name and occupation of the parents, lists "William Wood, Surgeon, F.R.S. & L.S." and "William Daniell, Artist, R.A.", a reflection of the social structure of the time. It is also possible that William and Juliana had other children for who we found no records.

Taxa Named for William Wood

Three species appear to have been named for William Wood, only one now considered valid. *Pleurotoma woodii* Kiener, 1840, was an unnecessary new name for *Murex bicarinatus* W. Wood, 1828, which is in turn a synonym of *Turris cryptorraphe* (G. B. Sowerby I, 1825). *Chiton woodii* Clessin, 1903, was an unnecessary replacement name for *Chiton sulcatus* W. Wood, 1814, which is a senior primary homonym of *Chiton sulcatus* Quoy & Gaimard, 1835. *Defrancia woodiana* Møller, 1842, is a valid species of the turrid genus *Obesotoma* from Greenland.

There are many additional "*woodii*" and "*woodiana*" taxa that have other origins. For example, *Bulimulus woodianus*, *Cyclostoma woodiana*, and *Helix woodiana* Lea, 1834, and *Symphynota woodiana* and *Cyrena woodiana* Lea, 1840, were all named for a William W. Wood, then of Manila, who provided Lea with material. At least, *Tornatella woodii* Nyst, 1836, *Vermetus woodii* Mörch, 1862, and *Pleurodon woodii* Dall, 1898, were named for Searles Valentine Wood, and there are probably additional taxa named for him, including at least one *searleswoodii.*

WOOD'S MALACOLOGICAL WORKS

Additional details about some of these works are given in Appendix A, and they are included in the Literature Cited.

General Conchology (1814–1815)

The *General conchology* was issued in 12 or 13 parts from April 1814 until sometime in 1815, each part selling for 15 shillings. While the contents of most of the parts are known, their exact dates have yet to be discovered, although the first part was presumably issued in April 1814 (Iredale, 1922; Dance, 1972), and some species can bear that date. Because the dates of the rest of the parts are unknown, the species in all but the first part have to be dated as 1815.

The first and only volume in an intended series, this work contains only Bivalvia, Polyplacophora, and barnacles. There are figures and descriptions of 26 new bivalve species and eight new species of chitons. The new species were contained in the collections of Mrs. Sarah Mawe (1767–1846), the wife of John Mawe (1766–1829); Henry Constantine Jennings (1731–1819); Dr. Coombe, about whom we know little[10]; a Mrs. Robertson, about whom we know nothing; and the collection of the Linnean Society. In addition, Wood acknowledged access to the collection of George Brettingham Sowerby I (1788–1854), and in some cases, the source collection was not noted. In others, Wood cited figures in earlier literature. No specimens from this work are known. A search of the collections of the Linnean Society for the specimens of the four species figured as being in that institution proved fruitless (K. Way, personal communication, 1 July 2010). In the Preface, Wood stated that "the plates which accompany this work will be accurately drawn and engraved from specimens only." The 60 quarto plates are generally excellent, with the figures nicely arranged. Unfortunately, the identity of the artist is not known (Fig. 3).

This work was reissued in 1835 with a slight modification to the title (and deletion on p. 246 on some copies of "End of the First Volume"). Otherwise, the two printings are identical.

Index testaceologicus (1818)

This is the first appearance of this title, which appeared in several editions and forms. Wood's Preface makes it clear that it was not intended to be an original work, but was instead a simple list of species with references to previously published figures.

The Linnaean molluscan genera, including tube-dwelling annelids under *Serpula* and barnacles under *Lepas*, were represented on eight plates by one or two figures, with only the genus name and a number representing the species number in the *Index*. These drawings were by Wood himself as shown by a small "WW" at the bottom of the plates. The figures are not of high quality, but they do not really deserve the comments of Wilkins (1957: 157) that "the figures are anything but neat, and mostly lack beauty" and "in fact having a decidedly amateurish appearance." Although in octavo format, the plates are not crowded.

In his Preface, Wood noted the publication of Dillwyn's *Descriptive catalogue* (1817), in which many pre-Linnaean names first became nomenclaturally available. However, it was not cited in Wood's *Index*, Wood noting that his citations were limited to "a few of the principal authors, whose figures have an established

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[10] Dr. Coombe was a collector who loaned material to James De Carle Sowerby (1781–1871) and George Perry (1771–18**) for illustrations.

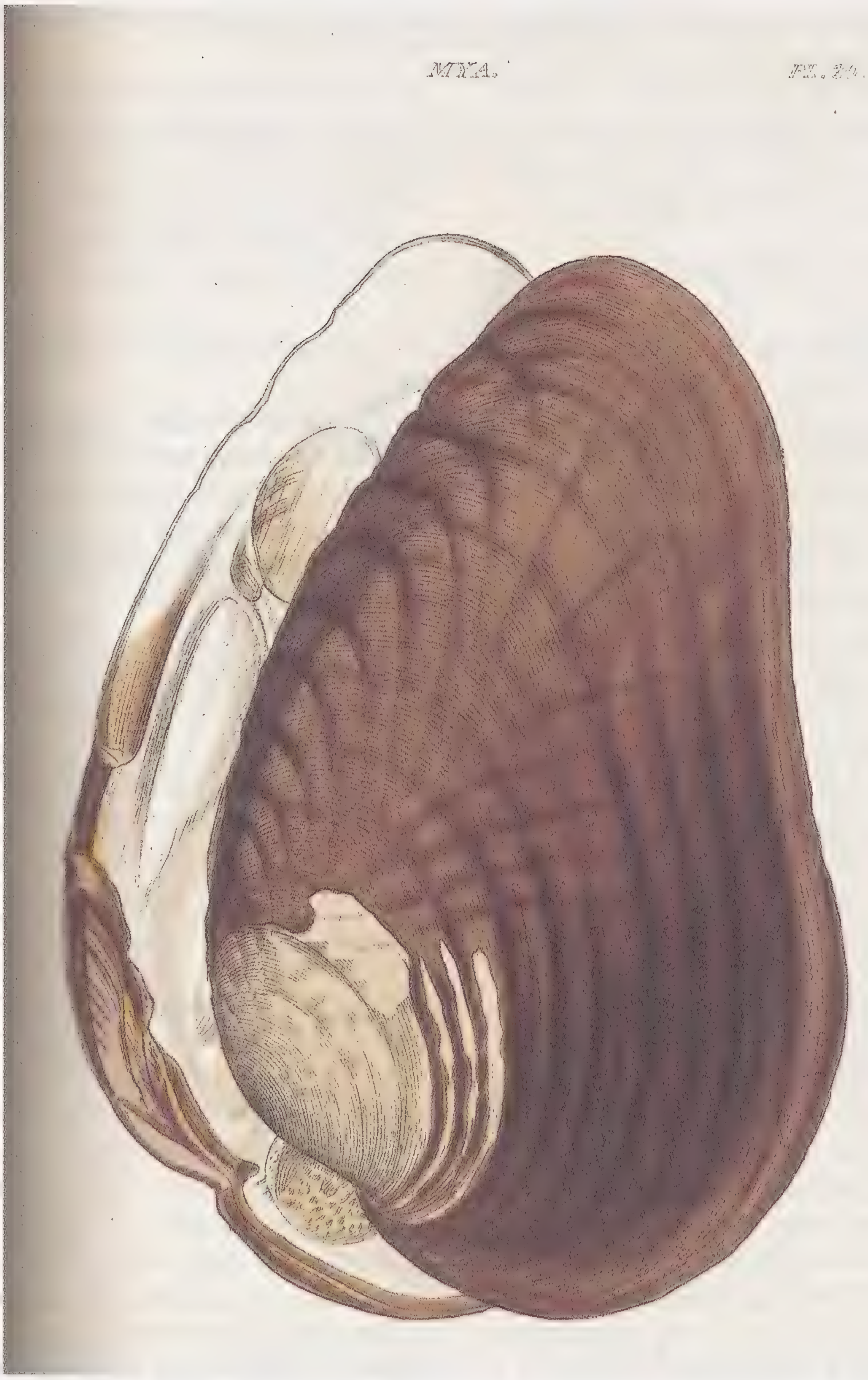


FIG. 3. Original figure of *Mya crassa* Wood, 1815: pl. 20. This specimen was stated to weigh one pound and six ounces. Described from an unknown locality, it is now known to be from Indo-China and is placed in the genus *Lamprotula.*

character for accuracy." This, together with the fact that Wood used only the limited number of Linnaean genera, confused compilers, such as Sherborn (1922–1932), as to where some species names first appeared. For example, previously unavailable Martini and Chemnitz names that first became available in Dillwyn (1817) or in other works under one genus may have appeared in Wood (1818) under a different genus and were thus listed by Sherborn as being Wood names. Also, a few Dillwyn names (e.g., *Turbo nodulosus*) were omitted by Sherborn. Only five species, all gastropods, first became available in this work, all based on earlier figures of Chemnitz and/or Lamarck. Four are synonyms, and one is apparently the valid name for a nassariid.

The text is arranged in six columns, the first being a number representing the number of the species in the genus being treated. The second column lists the Linnaean names. The third column is reserved for a page number in Gmelin if his work is referenced, and the fourth column is the vernacular English name for the species. The fifth column is headed Synonyms and lists the reference to which the name applies, followed by the final column for Habitat. The latter is not really habitat but country of origin and is often general. A long dash represents "ditto marks" or "same as above."

Index testaceologicus (1823–1825)

In 1823, Wood issued the first part of a second edition (not so noted on title page) of the *Index testaceologicus*, completed by a second part two years later (Wood, 1823–1825). A far more ambitious work, Wood attempted to figure every species with small drawings, either copied from the literature or based on specimens in the collections of James Sowerby, G. B. Sowerby I, and Emma Mawe. The eight plates of the 1818 edition were not reprinted in the 1823–1825 printing. The text of the two editions, except for prefatory material, is identical, as described in Appendix A.

The 37 plates, in octavo format [imprint area slightly variable but approximately 10.2 x 16.8 cm], have about 60 figures each. Although not mentioned in this edition, Wood later stated that the first six plates were produced by James Sowerby (1757–1822), the rest drawn by William Wood, Jr., and produced by William Wood himself (Wood, 1828a: iv). Because no species are described in words in this work, all depends on the figures. While very small, they were carefully drawn, generally from actual specimens, although a few were copied from earlier literature. All were realistically colored. Small letters and plus and dot symbols accompanying the figures indicate the size of the specimens involved: + indicated a half inch (13 mm); a + accompanied by a dot was three-quarters of an inch (19 mm); and letters of the alphabet, up to h, indicate inches. Thus, for example, c accompanied by a + and a dot would be two and three-quarters of an inch, or 95 mm. A number of subsequent workers, not having read Wood's preface, have wrongly cited these figures as, for example, "fig. 4c". Additionally, "n" denoted a specimen printed at natural size, and "m" denoted a magnified view, with a tiny additional figure added to denote the actual size.

No new species names seem to have been made available in the second edition of his *Index testaceologicus* (Wood, 1823–1825), in the subsequent edition three years later (1828a), or in his pamphlet the following year (1829a). However, because Wood in some cases figured the wrong species, names have been misattributed to him from this work. Here, we have considered these to be only misidentifications.

A second issue, differing in minor details from the original appeared in 1828 (Wood, 1828a), along with the far more important *Supplement*, which is discussed below. (Appendix A contains details on the differences between the 1818, 1823–1825, and 1828 versions.)

Index testaceologicus (1828a)

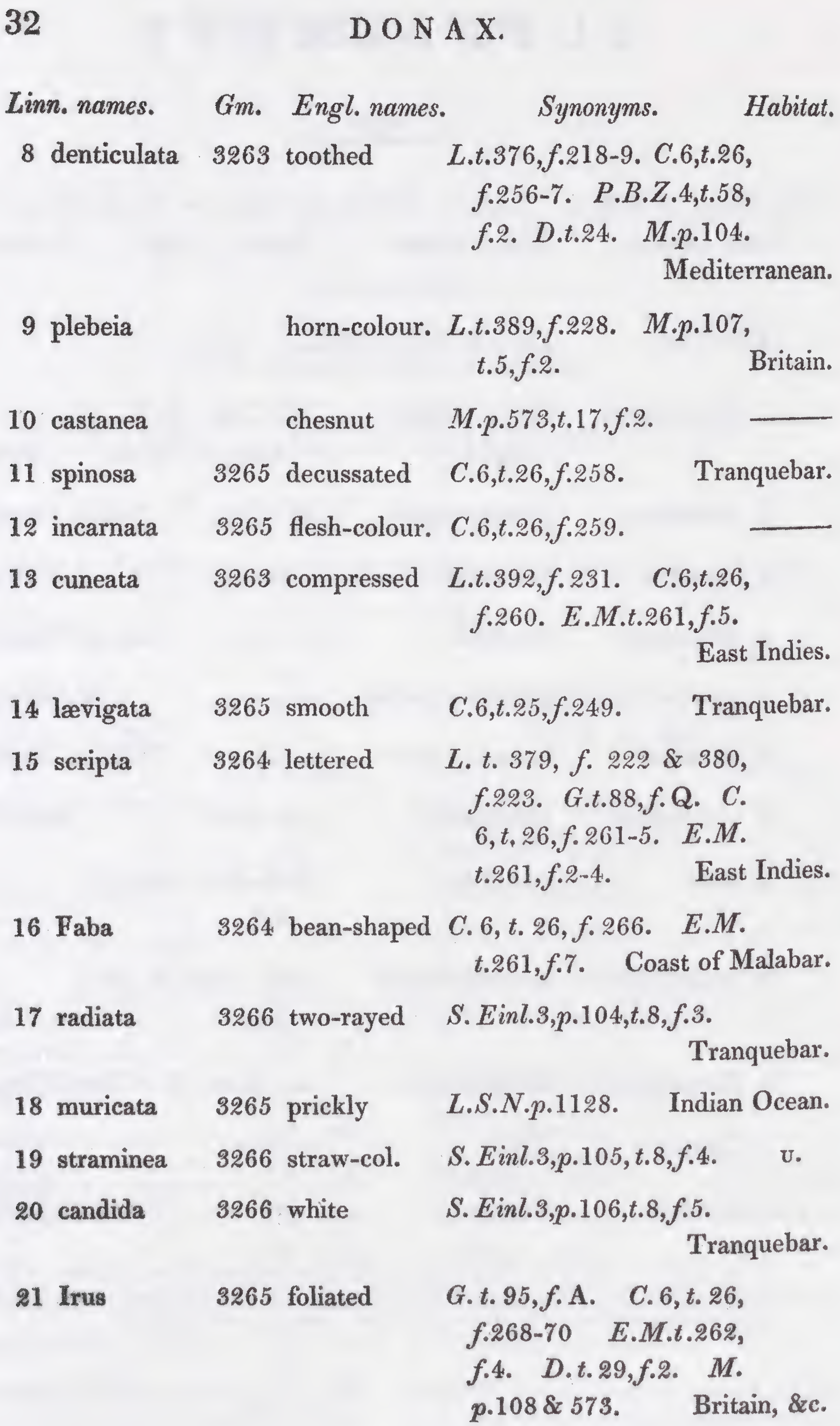
Stated on the title page to be "Second Edition, corrected and revised", the wording is almost identical to the 1823–1825 edition. A comparison of this printing with the previous one is given in Appendix A. A sample page is shown in Fig. 4.

Supplement to the Index testaceologicus (1828b)

This slender volume is by far Wood's most important malacological work, although it contains only eight plates. While the figures are very small, they were also carefully drawn by William Wood, Jr., generally from specimens, although a few were copied from earlier literature. All were realistically colored. Both the text and plates are arranged as in the *Index*, with long dashes representing ditto marks. Size markings are the same as in the earlier books (Fig. 5). Most of Wood's new species date from here. Unfortunately, this work is very confusing for several reasons.

Wood did not credit any of the names in this work to authors, so it proved difficult for subsequent workers to be sure which names are ones he took from published literature and which first appeared in this book. Wood had free access to several collections, most importantly those of the British Museum, J. E. Gray, and Emma Mawe. In those collections, many new species had been given manuscript names, the first two by J. E. Gray and the last by John or Emma Mawe, and Wood used these in his *Supplement*.In fact, Wood did not consider himself the author of any new name in the *Supplement*, as he stated:

> "It will be seen by a reference to the third column, that the majority of the shells have been figured from specimens in the British Museum, and the names attached to them in that collection have been adopted. For the rest, except such as have been derived from books, the Author gratefully acknowledges the assistance of Mrs. Mawe, and Mr. Gray, from whose Cabinets, and principally

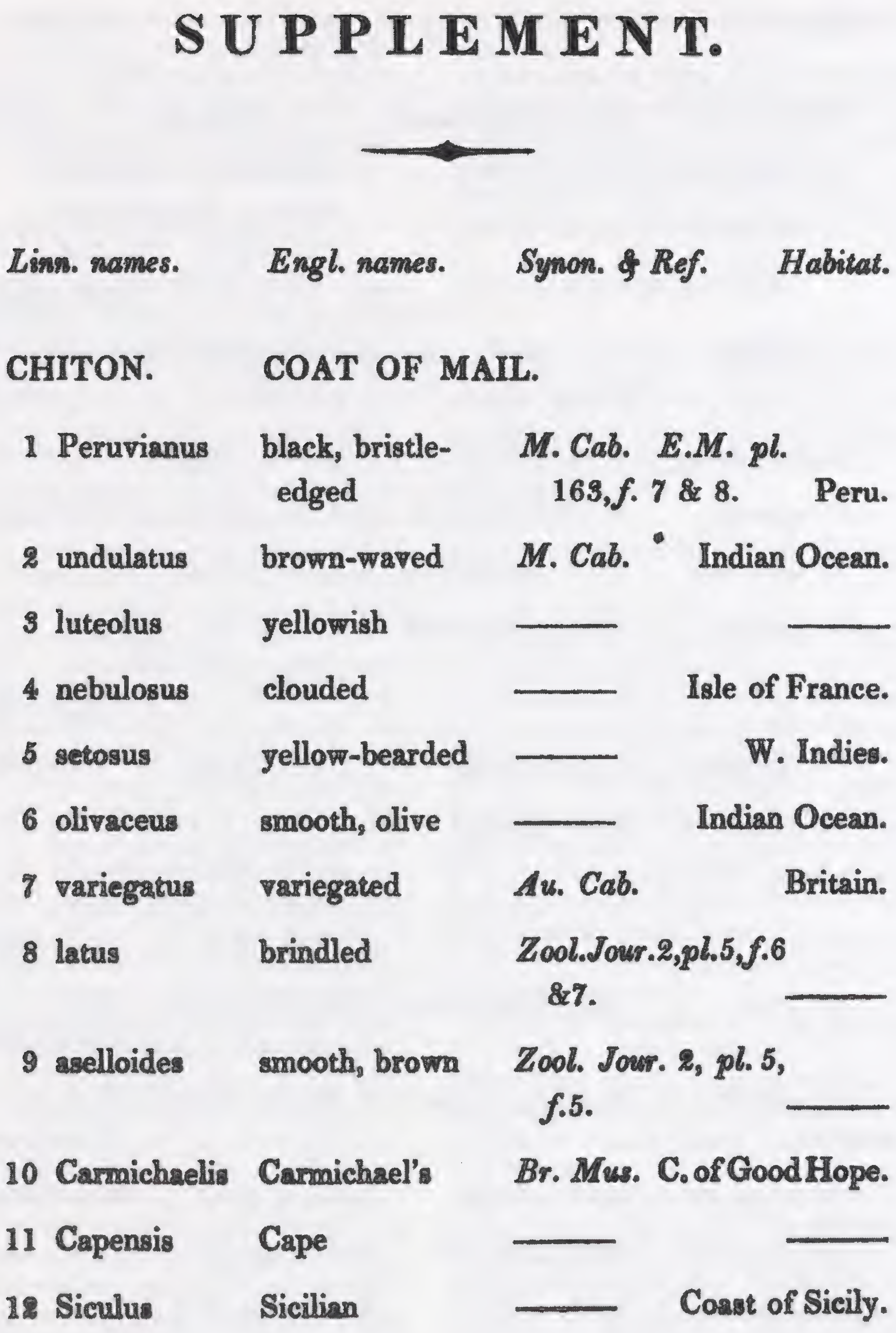


32

DONAX.

Linn. names.	*Gm.*	*Engl. names.*	*Synonyms.*	*Habitat.*
8 denticulata	3263	toothed	*L.t.*376,*f.*218-9. *C.*6,*t.*26, *f.*256-7. *P.B.Z.*4,*t.*58, *f.*2. *D.t.*24. *M.p.*104.	Mediterranean.
9 plebeia		horn-colour.	*L.t.*389,*f.*228. *M.p.*107, *t.*5,*f.*2.	Britain.
10 castanea		chesnut	*M.p.*573,*t.*17,*f.*2.	———
11 spinosa	3265	decussated	*C.*6,*t.*26,*f.*258.	Tranquebar.
12 incarnata	3265	flesh-colour.	*C.*6,*t.*26,*f.*259.	———
13 cuneata	3263	compressed	*L.t.*392,*f.* 231. *C.*6,*t.*26, *f.*260. *E.M.t.*261,*f.*5.	East Indies.
14 lævigata	3265	smooth	*C.*6,*t.*25,*f.*249.	Tranquebar.
15 scripta	3264	lettered	*L. t.* 379, *f.* 222 & 380, *f.*223. *G.t.*88,*f.* Q. *C.* 6,*t.* 26,*f.* 261-5. *E.M.* *t.*261,*f.*2-4.	East Indies.
16 Faba	3264	bean-shaped	*C.* 6, *t.* 26, *f.* 266. *E.M.* *t.*261,*f.*7.	Coast of Malabar.
17 radiata	3266	two-rayed	*S. Einl.*3,*p.*104,*t.*8,*f.*3.	Tranquebar.
18 muricata	3265	prickly	*L.S.N.p.*1128.	Indian Ocean.
19 straminea	3266	straw-col.	*S. Einl.*3,*p.*105,*t.*8,*f.*4.	u.
20 candida	3266	white	*S. Einl.*3,*p.*106,*t.*8,*f.*5.	Tranquebar.
21 Irus	3265	foliated	*G. t.* 95,*f.* A. *C.* 6, *t.* 26, *f.*268-70 *E.M.t.*262, *f.*4. *D. t.* 29,*f.*2. *M.* *p.*108 & 573.	Britain, &c.

FIG. 4. Page 32 from Wood's *Index* (1828a) showing the arrangement. The abbreviations in the Synonyms column are identified in the Preface. The long blank lines are the same as ditto marks and indicate that the Habitat is the same as the preceeding.



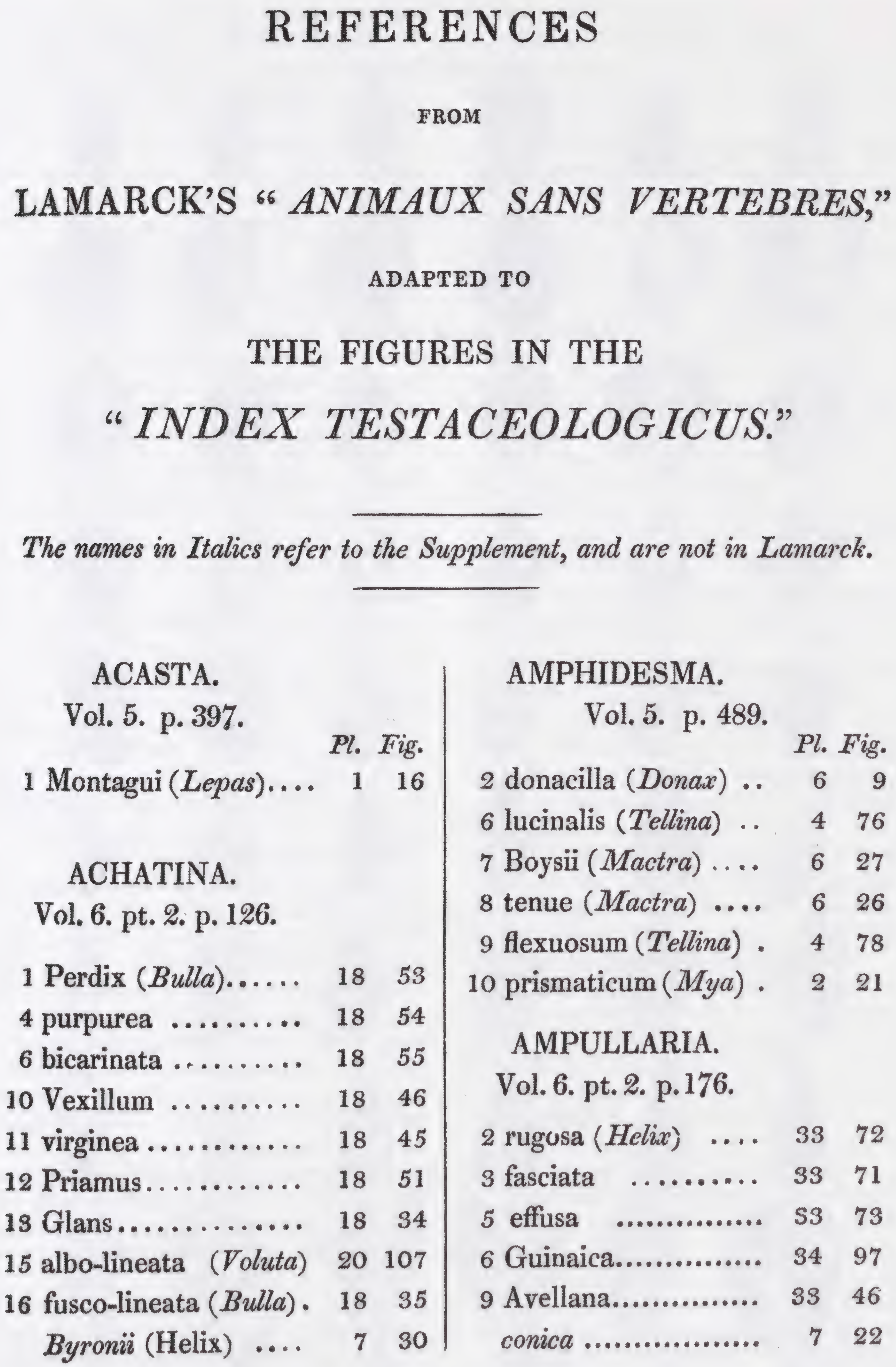
SUPPLEMENT.

Linn. names.	*Engl. names.*	*Synon. & Ref.*	*Habitat.*
CHITON.	**COAT OF MAIL.**		
1 Peruvianus	black, bristle-edged	*M. Cab. E.M. pl.* 163, *f.* 7 & 8.	Peru.
2 undulatus	brown-waved	*M. Cab.*	Indian Ocean.
3 luteolus	yellowish	——	——
4 nebulosus	clouded	——	Isle of France.
5 setosus	yellow-bearded	——	W. Indies.
6 olivaceus	smooth, olive	——	Indian Ocean.
7 variegatus	variegated	*Au. Cab.*	Britain.
8 latus	brindled	*Zool.Jour.*2,*pl.*5,*f.*6 &7.	——
9 aselloides	smooth, brown	*Zool. Jour.* 2, *pl.* 5, *f.*5.	——
10 Carmichaelis	Carmichael's	*Br. Mus.*	C. of Good Hope.
11 Capensis	Cape	——	——
12 Siculus	Sicilian	——	Coast of Sicily.

FIG. 5. Page [1] of Wood's *Supplement* (1828b) showing the arrangement. Unlike the *Index* (Wood, 1828a), there is no column for Gmelin numbers as no species in the *Supplement* were considered to have been known to Gmelin.

> from the former, he has derived the most essential benefit" (Wood, 1828b: iii).

There was no *Code of Zoological Nomenclature* in 1828, and most authors considered a species name to be attributable to the person who first placed a name on a specimen. This was certainly true of the species in Wood's *Supplement*, and they were generally attributed to Gray or Mawe by many authors until the modern *Code* came into effect. Hanley (1856b) attributed the new names to either Mawe or Gray, and Pfeiffer (1852b: viii), in his list of references, cited "Gray, J. E. in Wood *Ind. testaceologicus. Suppl.* 1828". Carpenter (1857: 178; 1864:



REFERENCES

FROM

LAMARCK'S "*ANIMAUX SANS VERTEBRES,*"

ADAPTED TO

THE FIGURES IN THE

"*INDEX TESTACEOLOGICUS.*"

The names in Italics refer to the Supplement, and are not in Lamarck.

ACASTA.

Vol. 5. p. 397.

	Pl.	*Fig.*
1 Montagui (*Lepas*)....	1	16

ACHATINA.

Vol. 6. pt. 2. p. 126.

1 Perdix (*Bulla*)......	18	53
4 purpurea	18	54
6 bicarinata	18	55
10 Vexillum	18	46
11 virginea	18	45
12 Priamus............	18	51
13 Glans..............	18	34
15 albo-lineata (*Voluta*)	20	107
16 fusco-lineata (*Bulla*).	18	35
Byronii (Helix)	7	30

AMPHIDESMA.

Vol. 5. p. 489.

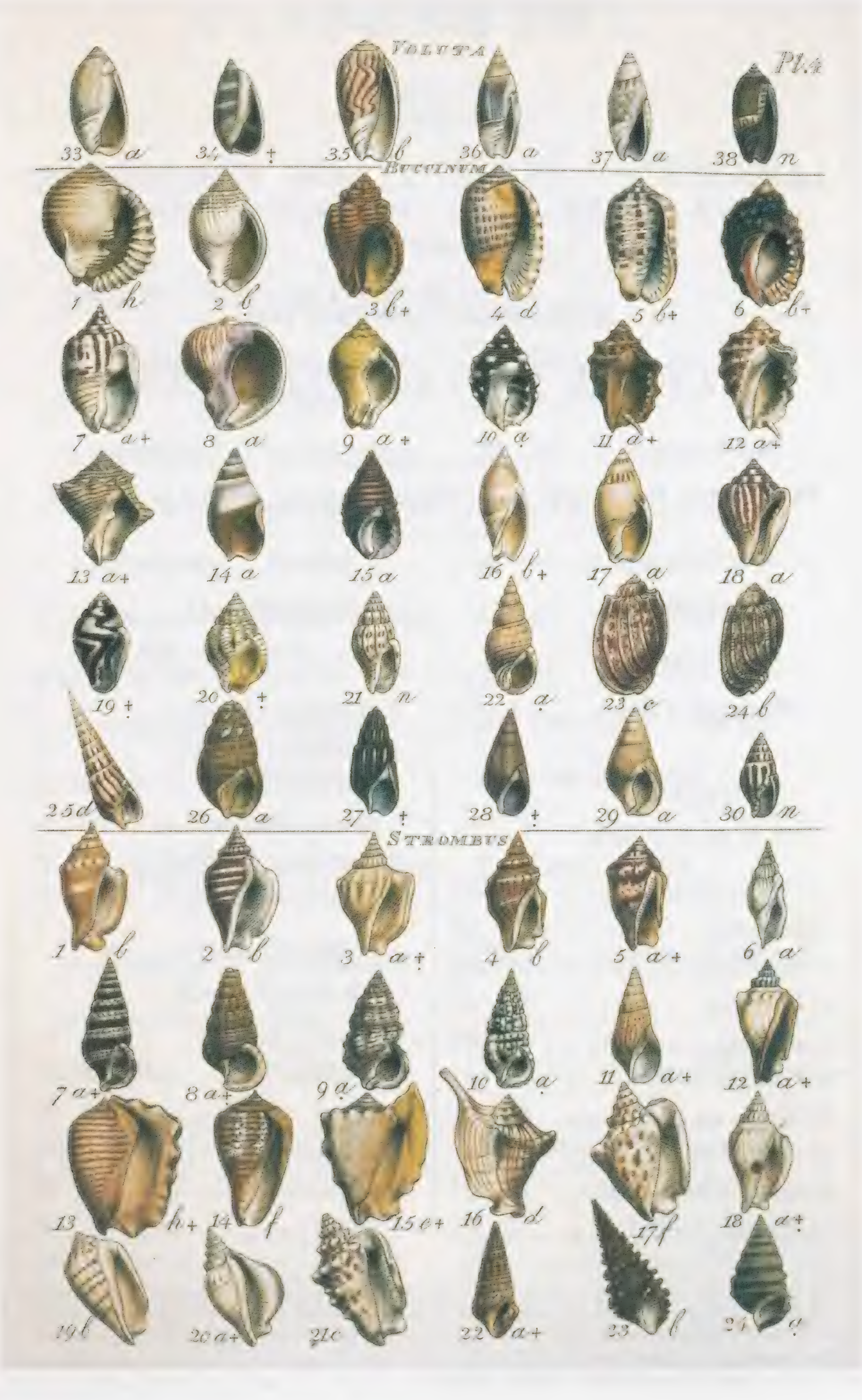
	Pl.	*Fig.*
2 donacilla (*Donax*) ..	6	9
6 lucinalis (*Tellina*) ..	4	76
7 Boysii (*Mactra*)	6	27
8 tenue (*Mactra*)	6	26
9 flexuosum (*Tellina*) .	4	78
10 prismaticum (*Mya*) .	2	21

AMPULLARIA.

Vol. 6. pt. 2. p. 176.

2 rugosa (*Helix*)	33	72
3 fasciata	33	71
5 effusa	33	73
6 Guinaica..............	34	97
9 Avellana..............	33	46
conica	7	22

FIG. 6. Page [29] of Wood's *Supplement* (1828b) showing the arrangement for species in the genera of Lamarck. Names not in italics refer to listings in the *Index* (1828a). The names in italics refer to species in the *Supplement*: for example, the listing for "*Byronii* (*Helix*)" indicates that this species was named *Helix byronii* in the Linnaean portion of the *Supplement*, but is here shown in the Lamarckian genus *Achatina*.


VOLUTA
Pl. 4
33 a
34 †
35 b
36 a
37 a
38 n
BUCCINUM
1 h
2 b
3 b+
4 d
5 b+
6 b+
7 a+
8 a
9 a+
10 a
11 a+
12 a+
13 a+
14 a
15 a
16 b+
17 a
18 a
19 †
20 †
21 n
22 a
23 c
24 b
25 d
26 a
27 †
28 †
29 a
30 n
STROMBUS
1 b
2 b
3 a †
4 b
5 a+
6 a
7 a+
8 a+
9 a
10 a
11 a+
12 a+
13 h+
14 f
15 e+
16 d
17 f
18 a†
19 b
20 a+
21 c
22 a+
23 b
24 g

523–524) quoted the eastern Pacific species named by Wood from the Mawe collection as having been named by Mawe. Gray considered himself to be the author of the species. In a bibliography he wrote in 1872, he listed as item 61 "The new species in the Supplement to 'Index Testaceologicus' of W. Wood, 1828." Gray's manuscript was later updated and printed by Saunders (1875) and this listing remained unchanged. The new species in the "Index" were also attributed to Gray in Agassiz' *Bibliographia Zoologiae et Geologiae* (Strickland, 1852). Even Sherborn (1922–1932), confused by the literature, credited some of the names to Gray. Such attribution is of course no longer appropriate, as Wood was responsible for the conditions that made the names available and is their author (ICZN *Code* Art. 50).

As in his earlier works, the species on pages 1–27 are arranged by Linnaean genera, which Wood regarded as primary, although most contemporary workers would have used post-Linnaean genera for many of them. Wood (1828b: iii) wrote: "It appears absurd that the word Linnean names, should be continued to shells wholly unknown to Linneus; yet as the arrangement is Linnean, the head could not well be dispensed with, without injury to the body". Wood provided a table on pp. 29–59, which had been supplied by Gray (Gray, 1867: 78), to allow users to see where the species in both his *Index* and the *Supplement* would fit within the scheme of Lamarck's genera, but he regarded these allocations of the species, new and old, as being secondary to their placement in the Linnaean genera. This final section is headed "References from Lamarck's "*Animaux sans Vertebres*," adapted to the figures in the "*Index Testaceologicus*" (Fig. 6). Some authors have thought that Wood created two nomina, one in a Linnaean genus and one in a Lamarckian genus, or assumed that the latter was correct. In at least one instance, the Lamarckian version of a name was selected as primary by "First Reviser" action. This is not correct, because Wood's new taxa are clearly established in the Linnaean genera and then, for convenience of some users, cross-referenced into Lamarckian genera.

An important downside of his approach was that the chances of creating homonyms was increased: fewer genera, more species names under each. Indeed, in some cases, Wood coined replacement names as a result of the homonyms he himself had created. For an example, see *Buccinum melanopsis* in the Melanopsidae.

In many cases, Wood undoubtedly intended to figure taxa of Lamarck, Dillwyn, or other authors, but figured specimens of other species in error. In some cases, the Wood taxa have been recognized as separate, sometimes homonymous taxa. Here we have adopted a conservative approach. Unless a name gained currency as separate, it is assumed to represent the earlier taxon, even if incorrectly depicted. Thus, if a single author many years ago decided that one of Wood's taxa was different than that of an earlier author, but modern authors have not recognized it as a separate taxon, then we have not done so. We have tried to deal with each taxon as an individual case, with the desire for nomenclatural stability being our primary concern.

There are no descriptions. Each species is given a scientific and a common name, the museum or private source of the specimen figured is listed, and the final column indicates the locality, if known. The horizontal lines in the last two columns are the equivalents of ditto marks. The species in each genus are numbered, and the numbers refer to the figures on the eight plates. Because more than one genus may appear on each plate, we have uniformly indicated throughout the genus as well as the figure number (Fig. 7). It should be noted that many localities proved to be erroneous, and there are also errors as to which collection the depicted specimens came from.

Wood proposed additional species names for taxa already named by G. B. Sowerby I in the *Tankerville Catalogue* (1825), a book specifically referenced by Wood. This was alluded to by Hanley (1856b: 197), who wrote about Wood's names: "In some few cases, they had been altered by the latter [Wood], at the suggestion of Dr. Goodall, from the presence of a similar name in the earlier portion of the 'Index,' &c. &c." This was clarified by Gray (1865: 29, footnote):

> "Many of the names of the shells in Wood's *Suppl.* were arbitrarily altered by the late Dr. Goodall as the work passed through the press, overlooking the fact that some of

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FIG. 7. Plate 4 of Wood's *Supplement* (1828b) showing the usual arrangement of six columns and ten rows, yielding 60 figures on the plate, with the plate divided into numerical sequences under each genus.

> them had been established by prior publication; and the proper names were given to the species in the MS, which was submitted to Dr. Goodall's inspection."

Rev. Joseph Goodall (1760–1840), who became Provost of Eton College, was in 1827 a Rector in West Ilsley, Berkshire, about 65 miles northwest of London (Stephen & Curthoys, 2004). Why Wood involved him but did not acknowledge his role is a mystery.

Gray (1867: 77–78) further discussed this matter:

> "...Mr. Blanford makes some observations on the various terminations which have been given to the name of the shell called *Assiminea Francesiae*. I may state that I originally described the shell as above, naming it after my sister, Frances Ince, who made a very extensive collection of the freshwater shells of India. ... It is figured by Mr. W. Wood, however, in the Supplement to the Catalogue of Shells as *Turbo Francesi*, from specimens sent home by Mrs. Ince: so the confusion began early. Mr. Wood, (unfortunately for science, as it added some confusion to the nomenclature) submitted the proofs of the Supplement to Dr. Goodall, who, I suppose, not knowing that the names which I had supplied to Mr. Wood had already been published (though it is mentioned in the preface that they are the names used in the British Museum collection), altered some of the names capriciously. I suppose that the Provost of Eton College did not think it right that a shell should be named after a woman; for in the same way he altered *Nerita Smithiae* and *Turbo Maugerae* to *Nerita Smithii* and *Turbo Maugeri*[11]. No one who knew him can believe that it arose from want of politeness or gallantry; but conchologists are more liberal now. I may observe that all of the shells figured from specimens in the Supplement were engraved (not etched) on the copper at once, from the shells selected by myself either from the British Museum, Mrs. Mawe's, or Mrs. Gray's collection; and I furnished him with the names of the species (which in some cases were so oddly changed) and also with the Lamarckian Index to the Catalogue and Supplement" [capitalization as published].

An example from one of Gray's synonymies (1865: 29) demostrates the above points [type faces as in the original]:

> Olivina lineolata B.M.
> Oliva lineolata, *Gray, in B.M.* 1827, *Beechey's Voy.* 131.
> Oliva Dama, *Goodall in Wood, Cat. Suppl.* t. 6. f. 37.

This illustrates Gray's attitude toward names he had applied to specimens in the British Museum collection. The "in B.M. 1827" can only mean that 1827 was the date Gray placed the name on a museum label. It was not actually published until its inclusion in Gray's portion of *Beechey's Voyage* (1839), and it is now regarded as a junior synonym of *Olivella dama* (W. Wood, 1828). Knowing that *dama* was not Wood's name, Gray attributed it to Goodall, who may have been responsible for replacing the name *lineolata* in Wood's manuscript.

Fossilia Hantoniensia (1829a)

The complete title of this work is *Fossilia Hantoniensia; or Hampshire fossiles, collected, and in the British Museum deposited, by Gustavus Brander, F.R.S. & F.A.S. London, 1776.* The title page bears the additional imprint: "The plates now reprinted, with a list of the figures, and references to the works of Lamarck and Sowerby." This is a reprint of the nine plates of this very rare and important work on the fossils of Hampshire, Wood evidently having acquired the original plates. He did not reprint the text, but listed each figure with its name and synonyms. Although he attributed the names, made available in 1776, to Brander, the original descriptions were written by Daniel Solander (1736–1782), to whom they are now attributed. Wood provided supplemental references for each species from Lamarck's works and from James and James De Carle Sowerby's *Mineral conchology of Great Britain* (1812–1846) as well as the names provided by these later authors for species not named by Solander.

Judging from its availability, this reprint must be as rare as the original. In 1829, it would have been important for all molluscan paleontologists, even those who owned the original. It remains a very useful work.

A list of the plates of the "Index Testaceologicus" (1829b)

This title was continued "with the Lamarckian names adapted to the figures in each plate." The list is arranged by plates. Beneath the heading is the statement:

> "Where the Numbers of the Figures are omitted, the Linnean and Lamarckian Generic and Specific Names are the same:

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[11] Such endings cannot be subsequently corrected unless there is evidence in the original publication that they were incorrectly formed (ICZN *Code* Art. 33).

> where they are retained, without being named, it is presumed that Lamarck had not noticed the Species in his 'Histoire Naturelle des Animaux sans Vertèbres'." [capitalization as published]

It appears that Wood received complaints about his use of the Linnaean genera, and he published this to make the Index more usable (and saleable). There is no title page. According to Reynell (1919: 89), it came with a green cover on which the title appeared as given above, the price [2*s*. 6*d*.], the date [1829] and the publisher [W. Wood, 428 Strand]. It appears to be a somewhat scarce item, but is available on the web.

Subsequent Editions of the *Index* by Hanley

Sylvanus Charles Thorp Hanley (1819–1899) received his degree and was admitted to the Inner Temple to study for the Bar. About that time, his father died, leaving Hanley financially independent. From then until his death Hanley, already interested in conchology, was an assiduous collector and author. Some of his works are laudable, especially the four volume *History of British Mollusca* (1848–1853) coauthored with Edward Forbes (1815–1854). His work on the Linnaean collection, *Ipsa Linnaei Conchylia*, should have been the definitive work on that collection. Dodge (1956: 240), in working on the same collection, wrote "the complexities of Hanley's involved language" and "his errors in reporting corrected, and his misleading punctuation clarified" among many other comments. A lack of clarity is an unfortunate component of almost all of Hanley's work.

Hanley had a predilection for taking a proprietary interest in the work of others, starting with his incorporation of unpublished parts of G. B. Sowerby I's *Species Conchyliorum* into his own *The Conchological Miscellany* (Petit, 2009: 17–18). In 1842a–1843 he published a "third edition" of Wood's *Index Testaceologicus*, with three plates not appearing in the original. This was immediately morphed into, and followed by (1842b–1856), *An illustrated and descriptive catalogue of Recent bivalve shells … forming an Appendix to the Index Testaceologicus.* This work contains 16 plates by Wood and Sowerby numbered 9–24 to follow the 8 in Wood's Supplement.

On a roll, Hanley then (1856b) published "*A new and completely revised* edition …" of Wood's *Index Testaceologicus*. Norris & Dance (2002: 367), who held a somewhat higher opinion of Hanley than do we, stated that "Hanley was the man chosen to edit a revised, enlarged edition in a larger format." The term "chosen" is puzzling in that Hanley had already published an "*Appendix*", as above mentioned. Also, Hanley's 1856 edition is "in larger format", only in that it is printed on slightly larger paper giving the plates and text a more pleasing margin. The plates are exactly the same size, as they were in fact the original plates.

In the Introduction to the 1856 edition, Hanley (1856b: ii) wrote: "As the whole of the letterpress, except the first column, (Wood's Linnean names) is entirely original, the writer should, perchance, have styled himself the Author, rather than the Editor; yet, as the text, in the present work, is avowedly subsidiary to the engravings, he has contented himself with the less honoured appellation." The title page does not contain the word "editor". Instead, after the long title, the authorship is given as "by Sylvanus Hanley, B.A., F.L.S."

The text in 1856b is arranged in only three columns: Wood's Linnean names, Lamarckian Genus, and Authority–Synonyms–Locality. The locality is in italics under the other matter in that column. Hanley's cryptic "synonyms" are, charitably, confusing. A simple example under the heading *Voluta* (p. 105) is:

> 119 *spiralis Pyramidella* Wood (as of Gm.! 3465) – *P. auriscati*, Adams, Sow. Th. ii. 812, pl. 172, fi. 1.

Although the specimen figured by Wood is not conspecific with the Rumphius figure cited by Gmelin, Wood had attributed the name to Gmelin and cited the same Rumphius figure. The name, even in a different genus, cannot be attributed to Wood as it is a simple misidentification (Article 49). This error was perpetuated by Tryon (1886: 305) who listed as *Pyramidella spiralis* Wood in synonymy.

The many misidentifications attributed to Wood by Hanley (1856b) are not included in the taxa list herein, unless we have noted such usage by others.

Detailed descriptions of Hanley's editions are given in Appendix B.

WOOD'S TAXA

The following is a list of the taxa that were made available by William Wood, whether or not currently considered valid (Table 1), as well as nomina that have been incorrectly attributed to him. The available names are in boldface at the beginning of each family. Those now considered valid, or that are probably or possibly valid, are indicated by an asterisk. Those lacking an aster-

TABLE 1. Availability and validity of Wood's taxa.

	Bivalves		Gastropods		Chitons		Totals	
Date of Work	Available	Also Valid	Available	Also Valid	Available	Also Valid	Available	Also Valid
1802	1	1	–	–	–	–	1	1
1814–1815	27	9	–	–	8	3	35	12
1818	–	–	5	1	–	–	5	1
1828b	40	15	195	79	6	1	241	95
Totals	68	25	200	80	14	4	282	109

isk are considered synonyms of earlier taxa, or are junior homonyms that have been supreseded by later synonyms or replacement names.

The list of taxa not in boldface under each family, with "W. Wood" in quotation marks, are those misattributed to Wood by Sherborn or other authors. If no attribution is given, the entry is the result of a Sherborn entry. We have not included those names expressly indicated by Sherborn as being transfers of earlier, non-Wood species from other genera. If a non-Wood name was attributed by some other author to Wood, we have indicated the source of the error. Also, this list contains some Wood mispellings of earlier taxa. In assigning species of Cardiidae to his newly introduced genera, Swainson (1840: 373–374) referenced figures in Wood (1815) in a manner indicating that they were Wood species, but Wood clearly referenced earlier authors. Sherborn noted most, but not all, of these names as being transfers from one genus to another, but he still inserted Wood's name. These non-Wood cardiids not treated herein are: *aeolicum, citrinum, flavum, fragum, oblongum, retusum,* and *unedo*.

Not included in this list are Wood's non-molluscan taxa, some of which were proposed in molluscan genera. For example, the bivalve genus *Anomia* contained brachiopods whereas the barnacles were described as *Lepas*. Because the brachiopod names proposed in *Anomia* would preoccupy any bivalves later named in that genus, we here note that the four involved are *A. dentata, A. ostreoides, A. rosea*, and *A. rubra*. We have not researched the validity of these brachiopod names.

BIVALVIA

The classification and order here follows that of Bieler et al. (2010).

NUCULANIDAE

tellinoides, Arca – "W. Wood", 1828b: 6, pl. 2, *Arca* fig. 5; 45, as *Nucula*. Name first made available as *Nucula tellinoides* G. B. Sowerby I, 1823. The western Atlantic *Adrana tellinoides* (G. B. Sowerby I, 1823) (Díaz & Puyana, 1994: 45).

YOLDIIDAE

glacialis, Arca – W. Wood, 1828b: 6, pl. 2, *Arca* fig. 6; 45, as *Nucula*. Loc: North Sea; NHMUK. *Non Arca glacialis* Gray, 1824. Synonym of *Portlandia arctica* (Gray, 1824) (Coan et al., 2000: 115). Type material not located in NHMUK in 2010.

MYTILIDAE

castaneus, Mytilus – "W. Wood", 1828b: 8, pl. 2, *Mytilus* fig. 3. This is *Mytilus castaneus* Lightfoot, 1786 [also = *Modiola castanea* Gray, 1825], which has been treated as a *nomen oblitum* to conserve the name of the Indo-Pacific *Arenofodiens vagina* (Lamarck, 1819) (Rehder, 1967: 13). This species was treated by Wilson (2006), without reference to the nomenclatural question.

elongatus, Mytilus – "W. Wood", 1818: 58, *ex* Chemnitz. Wood cited Chemnitz (1785: pl. 83, fig. 738), noting erroneously that the species came from the "Str. of Magellan", probably unaware that Fischer von Waldheim (1807: 245) had also picked up this Chemnitz name, in part for the same figure. After much speculation as to where this junior synonym belongs, the leading contender is considered to be *Perna perna* (Linnaeus, 1758) (M. Huber, 8 April 2010).

exustus, Mytilus – "W. Wood", 1818: 57. This is *Mytilus exustus* Linnaeus, 1758, a species of *Brachidontes*.

laevigatus, Mytilus – "W. Wood", 1828b: 8, pl. 2, *Mytilus* fig. 5; 1828b: 43, as *Modiola*. This is *Modiola laevigata* Gray, 1824, a junior synonym of *Musculus discors* (Linnaeus, 1767) (Coan et al., 2000: 168).

ARCIDAE

americana, Arca – W. Wood, 1828b: 6, pl. 2, *Arca* fig. 1. Loc.: Bay of Campeachy [= Campeche]; NHMUK. The synonymy of this species was discussed by Dall (1898: 650–652), who considered it a variety of *Arca campechiensis* Gmelin, 1791, a taxon placed in the synonymy of *Anadara ovalis* (Bruguière, 1789) by Abbott (1974: 424). Stevenson (1972: 202) listed it under "Type specimens not isolated in B.M.(N.H.)", and type material not located in NHMUK in 2010.

cylindrica, Arca – W. Wood, 1828b: 6, pl. pl. 2, *Arca* fig. 3. Loc.: unknown; NHMUK. Synonym of the European *Barbatia barbata* (Linnaeus, 1758) (Stevenson, 1972: 197). NHMUK 1969191, holotype.

nodosa, Arca – W. Wood, 1828b: 6, pl. 2, *Arca* fig. 8. Loc.: unknown; NHMUK. Listed in the literature as a synonym of various species, including as a senior synonym of *Anadara chemnitzii* (Philippi, 1851). Stevenson (1972: 202) listed under "Type specimens not isolated in B.M.(N.H.)", and type material not located in NHMUK in 2010. Best regarded as a *nomen dubium* at present.

****obliquata, Arca*** – W. Wood, 1828b: 6, pl. 2, *Arca* fig. 4. Loc.: unknown; NHMUK. *Barbatia* (*Savignyarca*) *obliquata* (W. Wood, 1828) from the Indian Ocean and Red Sea (Oliver, 1992: 36). Type species of *Savignyarca* Jousseaume, 1891, in that *S. savignyarca* Jousseaume, 1891, is a junior synonym of *B. obliquata*. NHMUK 1969190, holotype (Stevenson, 1972: 200; Kilburn, 1983: 520).

complanata, Arca – "W. Wood", 1818: 44. Name first made available by Bruguière, 1789.

imbricata, Arca – "W. Wood", 1818: 44. Name first made available by Bruguière, 1789, based on same figure in Chemnitz.

lacerata, Arca – "W. Wood", 1818: 44. Name first made available by Bruguière, 1789, as *A. lacerata*.

squamosa, Arca – "W. Wood", 1828b: 7, pl. 2, *Arca* fig. 12. Name first made available by Lamarck, 1819, for an Australian species of *Acar.* Lamprell & Healey (1998: 50) regarded it as a junior synonym of *Arca reticulata* Gmelin, 1791, which has been used for *Acar* species in several provinces. Because a type has not yet been found, it is best regarded as a *nomen dubium* (M. Huber, 8 April 2010).

GLYCYMERIDIDAE

pectiniformis, Arca – "W. Wood", 1828b: 7, pl. 2, *Arca* fig. 11; 47, as *Pectunculus*. Name first made available by Lamarck, 1819. A synonym of *Tucetona pectunculus* (Linnaeus, 1758) (Lamy, 1912: 85).

PTERIIDAE

morio, Mytilus – "W. Wood", 1818: 59. Name first made available by Dillwyn (1817) for a *Pteria*.

ISOGNOMONIDAE

folium, Mytilus – "W. Wood", 1828b: 8, pl. 2, *Mytilus* fig. 4. Name first made available as *Crenatula folium* Gray, 1825, type species, by monotypy, of *Dalacia* Gray, 1825 (a synonym of *Crenatula* Lamarck, 1803). *Crenatula folium* is a synonym of *C. picta* (Gmelin, 1791) (Wilkins, 1957: 151, 161).

PECTINIDAE

****muscosa, Ostrea*** – W. Wood, 1828b: 7, pl. 2, *Ostrea* fig. 2; 47, as *Pecten*. Loc.: South Sea; NHMUK. The western Atlantic *Aequipecten muscosus* (W. Wood, 1828) (Raines & Poppe, 2006: 298; Mikkelsen & Bieler, 2007: 142); type species (OD) of *Lindapecten* Petuch, 1995, which is now regarded as a junior synonym of *Aequipecten*. Type material not located in NHMUK in 2010.

tegula, Ostrea – W. Wood, 1828b: 7, pl. 2, *Ostrea* fig. 3. Loc.: unknown; collection of Mrs. Mawe. Synonym of the Australian *Scaeochlamys livida* (Lamarck, 1819) (Dijkstra, 1994: 492; Raines & Poppe, 2006: 230). Possible holotype, NHMUK 20100599, *ex* Cracherode collection.

asperrima, Ostrea – "W. Wood", 1828b: 7, *Ostrea* fig. 1; 47, as *Pecten*. Name first made available as *Pecten asperrimus* Lamarck, 1819.

gigantea, Ostrea – "W. Wood", 1828b: 7, pl. 8, *Ostrea* fig. 7. Name first made available as *Lima gigantea* Gray, 1825. The Californian *Crassadoma gigantea* (Gray, 1825) (Coan et al., 2000: 238).

ornata, Ostrea – "W. Wood", 1828b: 7, pl. 2, *Ostrea* fig. 4; 47, as *Pecten*. Name first made available as *Pecten ornatus* Lamarck, 1819.

SPONDYLIDAE

citreus, Spondylus – "W. Wood", 1818: 41. Name first made available by Gmelin (1791); now considered a *nomen dubium*.

LIMIDAE

scabra, Ostrea – 'W. Wood", 1818: 51. Name first made available as *Ostrea scabra* Born, 1778. The western Atlantic *Ctenoides scaber* (Born, 1778) (Mikkelsen & Bieler, 2003: 679–682; 2007: 130).

subauriculata, Ostrea – "W. Wood", 1828b: 7, pl. 2, *Ostrea* fig. 5; 41, as *Lima* (Sherborn). This name first made available by Montagu (1808). The European *Limatula subauriculata* (Montagu, 1808), type species of this genus (Bowden & Heppell, 1966: 107).

IRIDINIDAE

rostrum, Arca – W. Wood, 1828b: 6, pl. 2, *Arca* fig. 9. Loc.: unknown; NHMUK. Further on in the same work, Wood (1828b: 41) labeled this figure as *Iridina ovata*, presumably meaning the African *I. ovata* Swainson, 1823. Hanley (1856b: 205) also synonymized this name with *Iridina ovata* Swainson, 1823 (see also under *Iridina ovata* below). This African species is now listed as *Pleiodon ovatus* (Swainson, 1823) (Daget, 1998: 151). Type material not located in NHMUK in 2010.

elongata, Arca – "W. Wood", 1828b: 7, pl. 2, *Arca* fig. 10; 41, as *Iridina*. Name first made available as *Iridina elongata* G. B. Sowerby I, 1822. Synonym of *Mutella exotica* (Lamarck, 1819) (Haas, 1964: 598).

ovata, Iridina – "W. Wood", 1828b: 41. Sherborn (1929: 4654) misattributed this name to Wood, having missed its publication by Swainson (1823) five years earlier.

HYRIIDAE

angulata, Mya – W. Wood, 1828b: 3, pl. 1, *Mya* fig. 12; 40, as *Hyria corrugata*. Loc.: freshwater of South America; Mrs. Mawe. Synonym of *Prisodon corrugatus* (Lamarck, 1819) (Simone, 2006: 249). Wood evidently changed his mind on the identity of the figured specimen and abandoned his new name.

Castalea – An error in W. Wood (1829b: 29) for *Castalia* Lamarck, 1819.

UNIONIDAE

****crassa, Mya*** – W. Wood, 1815: 106, pls. 20, 21. Loc.: unknown; [H. C.] Jennings collection. *Lamprotula crassa* (W. Wood, 1815) from Indochina (Haas, 1969: 283); type species (OD) of *Gibbosula* Simpson, 1900, now treated as a junior synonym of *Lamprotula* Simpson, 1900.

gravis, Mya – W. Wood, 1828b: 3, pl. 1, *Mya* fig. 6; 57, as *Unio cariosus*. Loc.: freshwater of North America; Wood collection. Wood evidently decided that his specimen was actually *Unio cariosus* Say, 1817. However, *Mya gravis* is now considered to be a synonyn of the widespread North American *Actinonaias ligamentina* (Lamarck, 1819) (Parmalee & Bogan, 1998: 51–53).

****nodulosa, Mya*** – W. Wood, 1815: 106–107, pl. 22, figs. 1–4. Loc.: unknown; [H. C.] Jennings collection. The Chinese *Lamprotula nodulosa* (W. Wood, 1815) (Haas, 1969: 279).

oblongata, Mya – W. Wood, 1828b: 2, pl. 1, *Mya* fig. 2; 57, as *Unio*. Loc.: freshwater of North America; Wood collection. Synonym of *Lampsilis radiata* (Gmelin, 1791) (Johnson, 1970: 390).

rigida, Mya – W. Wood, 1828b: 3, pl. 1, *Mya* fig. 10; 57, as *Unio rigidus*?. Loc.: freshwater of North America; NHMUK. Synonym of *Elliptio complanata* (Lightfoot, 1786) (Johnson, 1970: 314). Type material not located in NHMUK in 2010.

rotunda, Mya – W. Wood, 1828b: 2, pl. 1, *Mya* fig. 1; 57, as *Unio "rotundatus"*. *Non U. rotundatus* Lamarck, 1819. Loc.: freshwater of North America; Wood collection. Synonym of *Obovaria subrotundata* (Rafinesque, 1820) (Parmalee & Bogan, 1998: 167–169).

rugulosa, Mya – W. Wood, 1828b: 3, pl. 1, *Mya* fig. 7; 57, as *Unio*. Loc.: freshwater of North America; Wood collection. Possible synonym of *Alasmidonta marginata* Say, 1818 (Parmalee & Bogan, 1998: 56–57).

alata, Mya – "W. Wood", 1828b: 2, pl. 1, *Mya* fig. 3; 57, as *Unio*. First made available as *Unio alatus* Say, 1817; now *Potamilus alatus* (Say, 1817) (Parmalee & Bogan, 1998: 196–198).

cariosus, Unio – "W. Wood", 1828b: 57. Name first made available as *U. cariosus* Say, 1817, now *Lampsillis cariosa* (Say, 1817) from North America (Johnson, 1970: 382).

nasuta, Mya – "W. Wood", 1828b: 3, pl. 1, *Mya* fig. 4; 57, as *Unio*. Name first made available as *Unio nasuta* Say, 1817, now *Ligumia na-*

suta (Say, 1817) from North America (Johnson, 1970: 380).

obliqua, Mya – "W. Wood", 1828b: 3, pl. 1, *Mya* fig. 8; 57, as *Unio*. Name first made available as *Unio obliqua* Lamarck, 1819, the identity of which is uncertain. The North American species involved is now *Pleurobema cordatum* (Rafinesque, 1820) (Parmalee & Bogan, 1988: 180–181).

praelonga, Mya – "W. Wood", 1828b: 3, pl. 1, *Mya* fig. 11; 57, as *Unio*. Name first made available as *Unio praelongus* Barnes, 1823, which is now regarded as a synonym of *Ligumia recta* (Lamarck, 1819) (Parmalee & Bogan, 1988: 152–154).

undulatus, Mya – "W. Wood", 1828b: 3, pl. 1, *Mya* fig. 5; 57, as *Unio*. Name first made available as *Unio undulatus* Say, 1817, now regarded as a North American species of *Alasmidonta* (Clarke, 1981: 38).

LUCINIDAE

childreni, Tellina – "W. Wood", 1828b: 3, pl. 1, *Tellina* fig. 1. Name first made available as *Lucina childrenae* Gray, 1824.

muricata, Tellina – "W. Wood", 1815: 18. Name first made available by Spengler (1798). The western Atlantic *Lucinisca muricata* (Spengler, 1798) (Mikkelsen & Bieler, 2007: 238).

scabra, Tellina "W. Wood", 1815: 184. Name first made available by Holten (1802). A synonym of the western Atlantic *Phacoides pectinata* (Gmelin, 1791) (Lamy, 1920b: 173).

CARDITIDAE

***tankervillii, Venericardia** – W. Wood, 1828b: 57, pl. 2, *Chama* fig. 4. Loc.: unknown; NHMUK. The west African *Cardita tankervillii* (W. Wood, 1828) (Abbott & Dance, 1982: 325, misspelled as "*tankervillei*"). Wood (1828b: 6) initially cited *Chama australis* [Lamarck, 1818], from "N[ew] Holland [Australia]; NHMUK", then decided that Lamarck's species was different and provided the name *tankervillii* for the NHMUK material. The name *Cardites tankervillii* (W. Wood, 1828) is in current use for the West African species, and the name *Cardita australis* Lamarck, 1818, is now regarded as a *nomen dubium* (M. Huber, email, 8 April 2010). NHMUK 1963638, holotype pair found during present study (ex Tankerville collection 354a).

ajar, Chama – "W. Wood", 1818: 42. Name first made available as *Cardita ajar* Bruguière, 1792, based on Chemnitz figure cited by Wood.

australis, Chama – "W. Wood", 1828b: 6, pl. 2, *Chama* fig. 4. Name first made available as *Venericardia australis* Lamarck, 1818. See discussion above under *tankervillii, Venericardia*.

crassicostata, Chama – "W. Wood", 1828b: 6, pl. 2, *Chama* fig. 5; 57, as *Venericardia*. Name first made available as *Cardita crassicostata* G. B. Sowerby I, 1825; the Panamic *Cardites crassicostata* (G. B. Sowerby I, 1825).

incrassata, Chama – "W. Wood", 1828b: 6, pl. 2, *Chama* fig. 3; 32, as *Cardita*. First made available as *Cardita incrassata* G. B. Sowerby I, 1825.

pectunculus, Chama – "W. Wood", 1818: 43. This is *Cardita pectunculus* Bruguière, 1792.

sulcata, Chama – "W. Wood", 1828b: 32. This seems to be *Cardia sulcata* Bruguière, 1792, a synonym of the Mediterranean *Cardita antiquata* (Linnaeus, 1758).

ASTARTIDAE

veneriformis, Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 8. Loc.: unknown; NHMUK. Synonym of the Arctic-Boreal *Astarte borealis* (Schumacher, 1817) (Coan et al., 2000: 287). A senior primary homonym of *Mactra veneriformis* Reeve, 1854, from Southeast Asia, for which *Mactra quadrangularis* Reeve, 1854, is an available replacement name (M. Huber, email, 8 April 2010). Type material not located in NHMUK in 2010.

ARCTICIDAE

icelandica, Venus – "W. Wood", 1818, 1823, 1828a: 35. An unjustified emendation of *Arctica islandica* (Linnaeus, 1767).

TRAPEZIDAE

angulata, Chama – "W. Wood", 1828b: 6, pl. 2, *Chama* fig. 1; 37, as *Cypricardia*. Name first made available as *Cypricardia angulata* Lamarck, 1819, a synonym of the Indo Pacific *Trapezium bicarinatum* (Schumacher, 1817) (Solem, 1954: 70–71). Wood, however, figured the wrong species, and Solem regarded his specimen as being the Indo-Pacific *Trapezium sowerbyi* (Hidalgo, 1903); the latter may be a junior synonym of *T. gilvum* (Martens, 1872) (Lamy, 1920a: 271–272). Wood's specimen was isolated in the NHMUK as a "holotype" of *Chama angulata* Wood (Wilkins, 1957: 162).

rostrata, Chama – "W. Wood", 1828b: 6, pl. 2, *Chama* fig. 2; 37, as *Cypricardia*. Name first made available as *Cypricardia rostrata*

Lamarck, 1819, a synonym of the Indo-Pacific *Trapezium bicarinatum* (Schumacher, 1817) (Solem, 1954: 68).

CARDIIDAE

citrinum, Cardium – W. Wood, 1815: 223, pl. 54, fig. 3. The 1815 treatment was overlooked by Sherborn, who cited this species from Wood (1825). Loc.: "Mediterranean, the Indian Ocean, the coast of South America, and the shores of the West India islands"; figured specimen from Linnean Society collection. Wood also cited *Cardium serratum* Linnaeus, 1758, of which it is now regarded as a synonym (McLean, 1939: 168). The western Atlantic species *Laevicardium serratum* (Linnaeus, 1758) has been nomenclaturally entangled with the Indo-Pacific *Fulvia laevigatum* (Linnaeus, 1758). Type specimen of *Cardium citrinum* not located in Linnean Society in 2010.

fimbriatum, Cardium – W. Wood, 1815: 234–235, pl. 56, figs. 4, 5. Loc.: unknown; figured specimen from [H. C.] Jennings collection. Synonym of the Asian *Vepricardium coronatum* (Spengler, 1799) (Vidal, 2000: 450–451; Hylleberg, 2004: 513).

maculosum, Cardium – W. Wood, 1815: 218–219, pl. 52, fig. 3. Loc.: unknown ["Ceylon" (Hylleberg, 2004: 610)]; figured specimen from Mrs. Mawe. Type not located in NHMUK (Hylleberg, 2004: 610). Wood also cited Lamarck (1816: pl. 298, fig. 6). The IndoPacific *Acrosterigma maculosum* (W. Wood, 1815) (Hylleberg, 2004: 610–612; Poorten, 2009: 17).

rigidum, Cardium – W. Wood, 1815: 236, pl. 57, figs. 2, 3. Loc.: unknown; figured specimen from Linnean Society. *Nomen dubium* (J. J. ter Poorten, email, 9 January 2010). Possibly a *Cerastoderma*. Type specimen not located in Linnean Society in 2010.

pecteniforme, Cardium – "W. Wood", 1815: 233–234; 1818: 27. Name first made available by Born (1780). The Indo-Pacific *Vasticardium pectiniforme* (Born, 1780) (Hylleberg, 2004: 688–689, as misspelled by Wood).

ringens, Cardium "W. Wood", 1815: 219–200, pl. 53, figs. 1, 2. Name first made available by Bruguière (1789: 225). The west African *Bucardium ringens* (Bruguière, 1789) (Keen, 1980: 6; Hylleberg, 2004: 738–739).

soleniforme, Cardium – "W. Wood", 1815: 233, pl. 56, fig. 3. Name first made available by Bruguière, 1789, now *Papyridea soleniformis* (Bruguière, 1789) from the western Atlantic. Wood mistakenly figured a specimen of *Papyridea lata* (Born, 1778). Wood's concept became the type species of *Papyridea* Swainson, 1840, through the subsequent designation of Gray (1847: 185) of *Cardium soleniforme* ["Wood"], as it was understood by Swainson and Gray. Watters (2002) discussed these two species in detail.

CHAMIDAE

lazarus, Chama – "W. Wood", 1818: 43. The Indo-Pacific *Chama lazarus* Linnaeus, 1758.

CYRENIDAE

similis, Venus – W. Wood, 1828b: 5, pl. 2, *Venus* fig. 5. Loc.: China; NHMUK. Initially thought to be a *Geloina* (Petit & Coan, 2008: 228–229), now believed to be a senior synonym of *Cyrena woodiana* Lea, 1834 (M. Huber, email, 31 Oct. 2010). Also a senior synonym of *Corbicula subsulcata* Clessin, 1878, type species, by original designation, of *Cyrenobatissa* Suzuki & Oyama, 1943. Thus, this species should be *Corbicula* (*Cyrenobatissa*) *similis* (W. Wood, 1828). NHMUK 20100626, holotype, located by M. Huber in 2010.

childreni, Venus – "W. Wood", 1828b: 5, *Venus* fig. 5. Name first made available as *Cyrena childrenae* Gray, 1825. Synonymized with the Philippines *Batissa laevigata* (Schumacher, 1817) by Prime (1878: 45).

cyprinoides, Venus – "W. Wood", 1828b: 5, pl. 2, *Venus* fig. 14. Name first made available as *Cyrena cyprinoides* Gray, 1825, the Asian type species of *Villorita* Gray in Griffith & Pidgeon, 1833 (Petit & Coan, 2008: 228).

MACTRIDAE

cyprinus, Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 1. Loc.: Peru; NHMUK. Long assumed to be a synonym of the western Atlantic *Mactra lineata* Say, 1822 (Wilkins, 1957: 164–165), which is a junior synonym of *Anatina anatina* (Spengler, 1802). However, it has been shown to actually be from Peru (Keen, 1961). The holotype, NHMUK 20100608, originally in the Calonne collection, passed through the hands of George Humphrey and then to Cracherode.

recurva, Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 2. Loc.: unknown; NHMUK. Synonym of the western Atlantic *Anatina anatina* (Spengler, 1802) (Keen, 1961). Holotype:

NHMUK 20100621 from the Cracherode collection (Wilkins, 1957: 165, pl. 25, fig. 12).

similis*, *Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 5. Loc.: not stated; NHMUK. *Non Mactra similis* Say, 1822. Synonym of the American boreal *Mactromeris polynyma* (Stimpson, 1860) (Coan et al., 2000: 454). Type material not located in NHMUK in 2010.

tenera*, *Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 4. Loc.: Van Dieman's L[and] = [Tasmania]; NHMUK. Synonym of the western Pacific *Spisula* (*Notospisula*) *aspersa* (G. B. Sowerby I, 1825) (Lamprell & Whitehead, 1992: pl. 39), more recently placed in genus *Pseudoxyperas* in Japan (Matsukuma in Okutani et al., 2000: 967). NHMUK 1996440, holotype (mentioned, without number, by Wilkins, 1957: 164); also holotype of *Mactra aspersa*.

alata, Mactra – "W. Wood", 1828b: 4, pl. 1, *Mactra* fig. 7. Name first made available by Spengler (1802). The western Atlantic *Mactrellona alata* (Spengler, 1802) (Wilkins, 1957: 162; Díaz & Puyana, 1994: 85, as *Mactra* (*Mactrellona*) *alata*).

subplicata, Mactra – "W. Wood", 1828a: 4, pl. 1, *Mactra* fig. 6. Name first made available by Lamarck, 1818. According to Gray (1837: 372), Wood mistakenly figured *Mactra plicataria* Linnaeus, 1767. Lamarck's species is now regarded as a synonym of *Mactrinula striatula* (Linnaeus, 1767).

MESODESMATIDAE

subtriangulata*, *Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 10. Loc.: not stated; NHMUK. The New Zealand *Paphies* (*Paphies*) *subtriangulata* (W. Wood, 1828) (Beu & de Rooij-Schuling, 1982: 214–218; Petit & Coan, 2008: 231). NHMUK 19821, holotype.

taprobanensis*, *Mactra – W. Wood, 1828b: 4, pl. 1, *Mactra* fig. 12. Loc.: Ceylon; NHMUK. *Non M. taprobanensis* Preston, 1904. Synonym of the Indo-Pacific *Mactra glabrata* Gmelin, 1791, now *Atactodea striata* (Gmelin, 1791), the type species of *Atactodea* Dall, 1895, a replacement name for *Paphia* Lamarck, 1799, *non* Röding, 1798 (Beu, 1971: 121). Not to be confused with *Mactra taprobaensis* Preston, 1904, an unrelated mactrid. Type material of Wood's species not located in NHMUK in 2010.

denticulata, Mactra – "W. Wood", 1828b: 4, pl. 1, *Mactra* fig. 9. Name first made available by Gray, 1825; synonym of *Mesodesma deauratum* (Turton, 1822) (Petit & Coan, 2008: 231).

ovata, Mactra – "W. Wood", 1828b: 4, pl. 1, *Mactra* fig. 11. Name first made available as *Erycina ovata* Gray, 1825, a junior synonym of the New Zealand *Paphies australis* (Gmelin, 1791) (Lamy, 1914: 39).

TELLINIDAE

acuta*, *Tellina – W. Wood, 1815: 157–158, pl. 44, fig. 1. Loc.: "West Indies" [restricted to St. Croix, Virgin Islands (Boss, 1966: 249)]. Synonym of *Tellina* (*Laciolina*) *magna* Spengler, 1798 (Boss, 1966).

alba*, *Tellina – W. Wood, 1815: 166. Based on Chemnitz (1782: pl. 11, fig. 98), whose specimen was from the Moltke collection. This seems to be a synonym of the Mediterranean *Tellina* (*Peronaea*) *planata* Linnaeus, 1758. Chemnitz's figure 98 was cited by Hanley (1846: 276) as being a variety of this species. This same figure was also cited by Dillwyn (1817: 85) under the name *Tellina flavescens*, which he thus made available from Chemnitz; in his synonymy, Dillwyn cited *Tellina alba* Wood.

convexa*, *Tellina – W. Wood, 1828b: 3, pl. 1, *Tellina* fig. 2. Loc.: New Holland [Australia]; NHMUK. Synonym of the Indo-Pacific *Tellina remies* Linnaeus, 1758 (Hanley, 1856b: 201). Type material not located in NHMUK in 2010.

dentata*, *Tellina – W. Wood, 1815: 195–196, pl. 46, fig. 7. Loc.: not stated. Figured specimen from the collection of Mrs. Mawe. The western Atlantic *Divaricella dentata* (W. Wood, 1815) (Mikkelsen & Bieler, 2007: 2380.

elegans*, *Tellina – W. Wood, 1828b: 4, *Tellina* fig. 5. Loc.: unknown; Mrs. Mawe. *Non Tellina elegans* Deshayes, 1824. *Tellina chariessa* Salisbury, 1934 (p. 84), was proposed as a replacement name for Wood's species, which occurs in the Seychelles.

interrupta*, *Tellina – W. Wood, 1815: 146, pl. 36, fig. 3. Loc.: "Indian and American Seas" [restricted to St. Kitts, Virgin Islands (Boss, 1966: 243)]. "Types lost" (Boss, 1966: 243). Synonym of the western Atlantic *Tellinella listeri* (Röding, 1798) (Boss, 1966: 243–247, as *Tellina*). Species figured in Mikkelsen & Bieler (2007: 328–329).

laevis*, *Tellina – W. Wood, 1815: 181, pl. 37, fig. 1. Loc.: West Indies [restricted to Kingston, Jamaica (Boss, 1966: 251)]; [H. C.] Jennings collection. Junior synonym of *Tellina fausta* Pulteney, 1799 (Boss, 1966: 251).

lutea, Tellina – W. Wood, 1828b: 3, pl. 1, *Tellina* fig. 3. Loc.: unknown; NHMUK. The North Pacific *Tellina lutea* W. Wood, 1828 (Coan et al., 2000: 403). NHMUK 20100590, holotype found during this study, *ex* Tankerville collection.

nivea, Tellina – W. Wood, 1815: 177, pl. 46, fig. 1. Loc.: "American ocean"; Mrs. Mawe. Possible synonym of the southeast Asian *Tellina sinuata* Spengler, 1798 (Hanley, 1846: 293).

sanguinea, Tellina – W. Wood, 1815: 159, pl. 44, fig. 2. Loc.: not stated; collection of Dr. Coombe. A *Tellina* of uncertain province (Coan & Valentich-Scott, 2005).

sulcata, Tellina – W. Wood, 1815: 178, pl. 47, fig. 1. Loc.: unknown. Figured specimen from Mrs. Mawe. *Non Tellina sulcata* Solander in Brander, 1766. This species occurs in the Red Sea and perhaps more widely in the Indo-Pacific (Oliver, 1992: 150). Oliver listed it as *Tellina* (*Serratina*) *sulcata* W. Wood, 1815, but that name cannot be used because it is a junior primary homonym. The next available name appears to be *Tellina belcheriana* G. B. Sowerby II, 1867 (pl. 34, fig. 190), which was based on a small specimen (Cooke, 1886: 105). Both MacAndrew (1870: 446) and Cooke (1886) listed this species as "*Tellina woodii* Desh.", but this name was not published by Deshayes. Perhaps aware of the homonymy, Deshayes may have written "*woodii*" on a label for future use as a potential replacement.

cordiformis, Tellina – "W. Wood", 1815: 191, pl. 43, figs. 4, 5. Name first made available by Holten (1802).

crystallina, Tellina – "W. Wood", 1815: 149. Name first made available as *Tellina cristallina* Spengler, 1798 (Boss, 1966: 261).

ochroleuca, Tellina – "W. Wood", 1828b: 4, pl. 1, *Tellina* fig. 6; 48, as *Petricola*. Name first made available as *Petricola ochroleuca* Lamarck, 1818, a synonym of the eastern Atlantic *Gastrana fragilis* (Linnaeus, 1758) (Nordsieck, 1969: 128).

DONACIDAE

madagascariensis, Donax – W. Wood, 1828b: 5, pl. 2, *Donax* fig. 3. Loc.: Madagascar; Mrs. Mawe. The east Africa *Donax* (*Grammatodonax*) *madagascariensis* W. Wood, 1828 (Oliver, 1992: 161, as "*madagascarensis*"); type species of the subgenus *Grammatodonax* Dall, 1900.

sexradiata, Donax – W. Wood, 1828b: 5, pl. 2, *Donax* fig. 5. Loc.: Isle of France [Mauritius]; Mrs. Mawe. Synonym of the European *Donax trunculus* Linnaeus, 1758 (G. B. Sowerby II, 1866: 317). Type material not found in NHMUK and best regarded as a *nomen dubium* (M. Huber, email, 8 April 2010).

biradiata, Donax – "W. Wood", 1828b: 5, pl. 2, *Donax* fig. 4; Isle of France [Mauritius]; Mrs. Mawe. This is *Donax biradiata* Forsskål, 1775. Stated by Hanley (1856b: 201) and Huber (2010: 691) to be a synonym of *Tellina trifasciata* Linnaeus, 1758, now *Donax trifasciata* (Linnaeus, 1758) from the Red Sea.

PSAMMOBIIDAE

amethystus, Solen – W. Wood, 1815: 138. pl. 34, fig. 1. Loc.: "India"; figured specimen from the collection of Mrs. Mawe. Wood also cited figures in Knorr (1772: pl. 12, fig. 2) and Chemnitz (1782: pl. 10, fig. 93). The Indo-Pacific *Gari* (*Psammobia*) *amethysta* (W. Wood, 1815) (Willan, 1993: 38–41). Mawe specimen not found in NHMUK in 1987 or 1989 (Willan, 1993: 38). Name on the Official List of Specific Names in Zoology (ICZN Opinion 910, 1970).

biradiata, Solen – W. Wood, 1815: 135, pl. 33, fig. 1. Loc.: unknown; figured specimen from the collection of Mrs. Mawe. The Indo-Pacific *Soletellina* (*Soletellina*) *biradiata* (W. Wood, 1815) (Willan, 1993: 77–79). Type specimen not found in the NHMUK in 1987 or 1989 (Willan, 1993: 77).

variegatus, Solen – W. Wood, 1815: 139, pl. 34, figs. 2–5. Loc.: unknown; Mrs. Mawe. Type material not located in NHMUK in 1989; regarded as a *nomen dubium* in Psammobiidae (Willan, 1993: 62).

lividus, Solen – "W. Wood", 1828b: 3, pl. 1, *Solen* fig. 3; 52, as *Sanguinolaria*. Name first made available as *Sanguinolaria livida* Lamarck, 1818, a synonym of the Australian *Soletellina* (*Soletellina*) *biradiata* (W. Wood, 1815) (Willan, 1993: 77–79).

SEMELIDAE

alba, Mactra – W. Wood, 1802: 165, 174, pl. 16, figs. 9–12. Loc.: Sandwich, England; [William] Boys. The European *Abra alba* (W. Wood, 1802); type species (subsequent designation of S. P. Woodward, 1854) of

Syndosmya Récluz, 1843, now generally regarded as a junior subjective synonym of *Abra* Lamarck, 1818.

decussata, Tellina – W. Wood, 1815: 190–191, pl. 43, figs. 2, 3. Loc.: unknown [restricted to St. Thomas, Virgin Islands (Boss, 1972: 8)]; figured specimen from the Linnean Society. Synonym of the western Atlantic *Semele proficua* (Pulteney, 1799) (Boss, 1972: 8–13). Type material not located in Linnean Society in 2010.

obliqua, Tellina – W. Wood, 1815: 152, pl. 41, figs. 4, 5. Loc.: not stated; figured specimen from the Linnean Society. Synonym of the western Atlantic and eastern Pacific *Semele* (*Amphidesma*) *purpurascens* (Gmelin, 1791) (Boss, 1972: 15–20; Coan, 1988: 20–21). Unnecessarily renamed *Amphidesma variabile* Gray, 1825. Suppressed for purposes of homonymy (ICZN Opinion 948, 1971). Type material not located in Linnean Society in 2010.

SOLECURTIDAE

tenuis, Solen – W. Wood, 1828b: 3, pl. 1, *Solen* fig. 5. Loc.: unknown; Mrs. Mawe. Type material not found in NHMUK in 1986 (S. Morris, pers. comm., 3 July 1986, to Cosel, 1993: 247) nor more recently (M. Huber, email, 8 April 2010). Possible synonym of either the southeast Asian *Sinonovacula constricta* (Lamarck, 1818) (Hanley, 1856b: 200, as *Solen*), or of *S. mollis* (G. B. Sowerby II, 1874). It is thus best regarded as a *nomen dubium* (M. Huber, email, 8 April 2010).

guineensis, Solen – "W. Wood", 1815: 129. Name first made available by Holten (1802) based on the same figure in Chemnitz (1795: pl. 198, fig. 1937). This name was quoted by Cosel (1993: 217) as a senior homonym of *Solen guinensis* Hanley, 1842, but credited to Wood. Although the spellings of the two names are different, Cosel unnecessarily proposed a replacement name for Hanley's taxon (ICZN *Code* Art. 58). Holten's species is a junior synonym of the west African *Solen adansoni* Bosc, 1801, the type species of *Tagelus* Gray, 1847.

VENERIDAE

***berrii, Venus** – W. Wood, 1828b: 5, 58, pl. 2, *Venus* fig. 2. Loc.: unknown; NHMUK. The Australian *Placamen berrii* (W. Wood, 1828) (Lamprell & Whitehead, 1992: pl. 62, species 470, as "*P. berryi* (Gray in Wood, 1828)"). NHMUK 20100607, 3 syntype pairs.

costulata, Venus – W. Wood, 1828b: 5, pl. 2, *Venus* fig. 15. Loc.: S[outh] Seas; Mrs. Mawe. Synonym of the Australian *Tawera gallinula* (Lamarck, 1818) (Fischer-Piette & Vukadinovic, 1977: 42–43).

***damaoides, Venus** – W. Wood, 1828b: 6, pl. 2, *Venus* fig. 17. Loc.: "East Indies"; NHMUK. Wood may have miscopied the label in the NHMUK, because when Gray published the species, it was named as *Trigona donacoides* Gray, 1838 (p. 304). The southeast African *Tivela damaoides* (W. Wood, 1828) (Fischer-Piette & P.-H. Fischer, 1942: 14–17). Holotype pair NHMUK 20100628, *ex* Cracherode collection (Wilkins, 1957: 166–167).

elegans, Venus – W. Wood, 1828b: 5, pl. 2, *Venus* fig. 3. Loc.: Brazil; NHMUK. *Non V. elegans* A. Adams & Reeve, 1850. Synonym of the western Atlantic *Leukoma pectorina* (Lamarck, 1818) (Hanley, 1856b: 203, as *Venus*). Type material not located in NHMUK in 2010.

hians, Venus – W. Wood, 1828b: 5, pl. 2, *Venus* fig. 11; 38, as *Cytherea*. Loc.: China; NHMUK. Not to be confused with *Meroe hians* Reeve, 1864, a species of *Sunetta* renamed *S. tumidissma* Tomlin, 1922 (p. 312), because of the homonymy. Wood's species is a synonym of the Indian *Sunetta solanderi* (Gray, 1825) (Fischer-Piette & Fischer, 1939: 211–212). Listed as "*Venus hynans* Solander, Wood" by Gray (1838: 303). NHMUK 20100623, *ex* Cracherode collection, holotype pair of both *hians* Wood and *solanderi* Gray.

pulchra, Venus – W. Wood, 1828b: 6, pl. 2, *Venus* fig. 16. Loc.: "S. Seas"; Mrs. Mawe. Synonym of the Indo-Pacific *Callista florida* (Lamarck, 1818) (Barnard, 1964: 503, as "*Pitaria*").

***stutchburii, Venus** – W. Wood, 1828b: 5, 58, pl. 2, *Venus* fig. 4; Loc: "Sandwich Isl." [Hawaii]; NHMUK. Attributed to the Hawaiian Islands in error (Kay, 1966), this is the New Zealand *Austrovenus stutchburyi* (W. Wood, 1828) (Powell, 1979: 426, as "*Chione* (*Austrovenus*)"; Beu, 2006: 278–287). The spelling "*stutchburyi*" has been considered a justified emendation, in that it was clearly proposed for Mr. Stutchbury (ICZN *Code* Art. 32; Beu, 2006: 281), a correction that has long been accepted. NHMUK 20050252/1–3, lectotype and 2 paralectotypes (Beu, 2006: 280).

***subrugosa, Venus** – W. Wood, 1828b: 5, pl. 2, *Venus* fig. 6; 37, as *Cytherea*, with fig. mistakenly given as 5. Loc.: Panama; Mrs. Mawe. The Panamic *Chione subrugosa* (W. Wood, 1828) (Keen, 1971: 190).

juvenilis, Venus – "W. Wood", 1818: 38. Name first made available by Gmelin, 1791.

kingii, Venus – "W. Wood", 1828b: 5, pl. 2, *Venus* fig. 9. Name first made available as *Cytherea kingii* Gray, 1826. The Australian *Callista kingii* (Gray, 1826).

lamellata, Venus – "W. Wood", 1828b: 5. Name first made available by Lamarck (1818).

ornata, Venus – "W. Wood", 1818: 36. Name first made available by Dillwyn (1817), based on same Chemnitz figures cited, among others, by Wood.

recens, Venus – "W. Wood". Higo et al. (1999: 510) listed this name in the synonymy of *Marcia marmorata* (Lamarck, 1818). However, this was an error for *Venus recens* Dillwyn, 1817, which is based on same Chemnitz figure. Indeed, the Chemnitz figure was first named as *V. recens* Holten, 1802, which appears to be the earliest available name. In any event, the name is not attributable to Wood.

reticulata, Venus – "W. Wood", 1818: 37. Name first made available by Linnaeus, 1758.

MYIDAE

globosa, Mya – W. Wood, 1815: 95, pl. 24, figs. 4–6. Loc.: unknown; Mrs. Mawe. Synonym of the west African *Tugonia anatina* (Gmelin, 1791) (Lamy, 1926: 153, but as "1843").

PHOLADIDAE

falcata, Pholas – W. Wood, 1815: 84, pl. 16, figs. 5–7. Loc.: not stated; collection of Dr. Coombe. Synonym of *Martesia* (*Martesia*) *striata* (Linnaeus, 1758) (Turner, 1955: 103).

ovum, Pholas – W. Wood, 1828b: 2, 48, pl. 1, *Pholas* fig. 4. Loc.: West Indies; NHMUK. Turner (1955: 104) considered this to be a synonym of *Martesia striata* Linnaeus, 1758, but it is instead the Southeast Asian *Pholadidea* (*Calyptopholas*) *ovum* (W. Wood, 1828) and a senior synonym of *P.* (*C.*) *chevey* Lamy, 1927 (M. Huber, email, 8 April 2010). NHMUK 20070600/1–5, syntypes, 4 pairs and 1 valve.

lancellata, Pholas – W. Wood, 1828b: 48. Spelling error for *P. lamellata* Turton, 1822.

HIATELLIDAE

picea, Mya – W. Wood, 1815: 96–97, pl. 22, fig. 5. Loc.: unknown. Figured specimen from collection of Dr. Coombe. Also cited Chemnitz (1795: pl. 198, fig. 1834). Synonym of the northwestern Atlantic *Cyrtodaria siliqua* (Spengler, 1793) (Lamy, 1924: 281).

SOLENIDAE

magnus, Solen – W. Wood, 1815: 130. Cited only Chemnitz (1782: pl. 5, fig. 35). Type species of *Cultellus* Schumacher, 1817. This Chemnitz figure was named *Solen maximus* Gmelin (1791: 3227), which is thus the senior synonym.The southeast Asian *Cultellus maximus* (Gmelin, 1791) (Swennen et al., 2001: 83).

truncata, Solen – W. Wood, 1815: 121, pl. 26, figs. 3, 4; pl. 27, fig. 2 (as "Var. β). Loc.: "American and Indian seas"; figured specimen from collection of Dr. Coombe. Wood also cited figures from nine non-binomial works. Figured as a western Indo-Pacific species (Abbott & Dance, 1982: 339; Rosenberg, 1992: 156), it is more likely a synonym of *S. ceylonensis* Leach, 1814 (Oliver, 1992: 136; Cosel, 1993: 217).

castrensis, Solen – "W. Wood", 1815: 134. Name first made available by Spengler (1794) (Cosel, 1990: 705–707; Willan, 1993: 53).

corneus, Solen – "W. Wood", 1828b: 3, pl. 1, *Solen* fig. 2. Name first made available by Lamarck, 1818, a western Pacific species.

linearis, Solen – "W. Wood", 1815: 121–122, pl. 27, fig. 2. Name first made available by Spengler (1794).

PHARIDAE

inflexus, Solen – W. Wood, 1815: 131, pl. 32, figs. 1, 2. Loc.: unknown; collection of Dr. Coombe. Senior synonym of the Southeast Asian *Siliqua* (*Neosiliqua*) *winteriana* (Dunker, 1853), which was figured in Abbott & Dance (1982: 340, as *Siliqua*) (M. Huber, email, 8 April 2010).

maximus, Solen – W. Wood, 1815: 129–130, pl. 31, fig. 3. Loc.: not stated. *Non S. maximus* Gmelin, 1791 (see above under *Solen magnus*). Synonym of the northeastern Pacific *Siliqua patula* (Dixon, 1789) (Coan at al., 2000: 448).

orbiculatus, Solen – W. Wood, 1828b: 3, 53, pl. 1, *Solen* fig. 4. Loc.: unknown; NHMUK. The southeast Asian *Orbicularia obiculatus* (W. Wood, 1828), of which it is the type species (Cosel, 1990: 292). Also the type species of the generic junior synonym *Elizia* Gray, 1854. NHMUK 1842.7.6.242 – 1 specimen, NHMUK 1842.9.23.25 – 1 specimen and NHMUK 20100592 – 1 specimen, possible syntypes located in present study.

politus, Solen – W. Wood, 1828b: 3, pl. 1, *Solen* fig. 6. Loc.: unknown; Mrs. Mawe. The Indo-Pacific *Siliqua polita* (W. Wood, 1828) (Oliver, 1992: 137).

THRACIIDAE

convexa, Mya – W. Wood, 1815: 92, pl. 18, fig. 1. Loc.: Devonshire, England. The European *Thracia* (*Homoeodesma*) *convexa* (W. Wood, 1815) (Coan, 1990: 30).

GASTROPODA

The classification and order here follows that of Frýda et al. (2005), except for some more recent changes within the Conoidea (J. Tucker, personal communication, 1 June 2010).

FISSURELLIDAE

laqueare, Patella – W. Wood, 1828b: 27, pl. 8, *Patella* fig. 6. Loc.: unknown; NHMUK. Regarded as a junior synonym of the western Atlantic *Hemitoma octoradiata* (Gmelin, 1791) by Hanley (1856b: 233) and by Krebs (1864: 86), who attributed the species to Gray. Type material not located in NHMUK in 2010.

crystallina, Patella – W. Wood, 1828b: 27, pl. 8, *Patella* fig. 8; 38, as *Emarginula*. Loc.: unknown; NHMUK. Placed with question in synonymy of the later *Emarginula cancellata* Philippi, 1836, by A. Adams (1852: 82), a species placed in turn in synonymy of the earlier *E. sicula* Gray, 1825. Wood's species name has disappeared from the literature and is not mentioned in modern chresonymies. *Emarginula sicula* (Gray, 1825) is a trans-Atlantic species, occurring in western Europe, the Mediterranean, and the western Atlantic (Abbott & Dance, 1982: 24). Type material not located in NHMUK in 2010, and type material of Gray's species has not yet been isolated either.

ambigua, Patella – "W. Wood", 1818: 182. New Holland. This is *Patella ambigua* Dillwyn, 1817, based on same Chemnitz figure, a species now placed in *Scutus*.

hiantula, Patella – "W. Wood", 1828b: 27, pl. 8, *Patella* fig. 7; 38, as *Fissurella*. This is *Fissurella hiantula* Lamarck, 1822.

HALIOTIDAE

corrugata, Haliotis –1828b: 26, pl. 8, *Haliotis* fig. 6. Loc.: unknown. NHMUK. A well-known species from southern California and Baja California (McLean, 1978: 11). Type material not located in NHMUK in 2010.

mariae, Haliotis – W. Wood, 1828b: 26, pl. 8, *Haliotis* fig. 5. Loc.: unknown; NHMUK. *Haliotis mariae* W. Wood, 1828, occurs in Yemen and Oman (Geiger & Poppe, 2000: 65). Type material not located in NHMUK in 2010.

tricostata, Haliotis – W. Wood, 1828b: 26, 39, pl. 8, *Haliotis* fig. 2. Loc.: unknown; NHMUK. Possibly a spelling error for *Haliotis tricostalis* Lamarck, 1822. Placed in the synonymy of the southern Australian *Haliotis scalaris* (Leach, 1814) by Geiger & Poppe (2000: 81), a senior synonym of *H. tricostalis*. NHMUK 1950.8.28.10 in the Cracherode collection that is the holotype of *H. scalaris* Leach (Wilkins, 1957: 163) is possibly also the holotype of Wood's species.

PATELLIDAE

intorta, Patella – "W. Wood", 1818: 179. Name first made available as *Patella intorta* Pennant, 1777, a synonym of *Ansates pellucida* (Linnaeus, 1758).

TROCHIDAE

aequalis, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 30; 51, as *Rotella*. Loc.: unknown; Gray. Placed in synonymy of the Indo-Pacific *R. vestiaria* (Linnaeus, 1758) [now placed in *Umbonium*] by Hanley (1856b: 220). Name not spotted in subsequent literature. NHMUK 20100587, 3 syntypes found in present study.

albidus, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 14. Loc.: Ireland; Wood collection. *Non Trochus albidus* Gmelin, 1791. Synonym of *Calliostoma zizyphinum* (Linnaeus, 1758) (Sabelli et al., 1990: 129).

armillatus, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 5. Loc.: S[outh] Seas; Mrs. Mawe. This Australian species, type of the subgenus *Salsipotens* Iredale, 1924, was treated as *Calliostoma* (*Salsipotens*) *armillatum* (W. Wood) by Wilson (1993: 63).

atratus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 25; 44, as *Monodonta atrata*. Loc.: unknown; NHMUK. Long recognized as occurring from Portugal to west Africa. Mistakenly placed in the synonymy of the West African *Monodonta punctulata* Lamarck, 1822, by Hanley (1856b: 220). Treated as *Osilinus* (*Pseudosilinus*) *atratus* (W. Wood) by Nordsieck (1982: 39, pl. 18, fig. 13.022) and as as *Osilinus atratus* (W. Wood) by Donald et al. (2005: 482). NHMUK 1987075, 2 syntypes.

badius, Trochus – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 46; 44, as *Monodonta*. Loc.: S[outh] Seas; Gray. From Australia; type of the genus *Phasianotrochus* P. Fischer, 1885. Junior synonym of *Phasianotrochus eximius* (Perry, 1811) (Wilson, 1993: 82). NHMUK 20100588, 3 syntypes found in present study.

byronianus, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 17; 44. Loc.: "Sandwich Islands"; NHMUK. Kay (1966) and McLean (1970: 123) settled the confusion caused by the incorrect locality and concluded that it is a synonym of the southern Caribbean *Tegula viridula* (Gmelin, 1791). NHMUK 20100625, probable holotype; NHMUK 20100627, 7 possible syntypes.

callosus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 33. Loc.: unknown; Gray. *Non Trochus callosus* Gmelin, 1791. Placed in the synonymy of *Trochus calliferus* Lamarck, 1822, by Hanley (1856: 21), an Australian species now placed in the genus *Monilea* (Wilson, 1993: 94). NHMUK 20100601, holotype.

***calyculus, Trochus** – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 44. Loc.: unknown; Gray. Treated as *Trochus* (*Monilea*) *calyculus* W. Wood from the Andaman Islands by E. A. Smith (1879: 818). NHMUK 1878.6.3.1, holotype.

***clanguloides, Trochus** – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 39. Loc.: unknown; Gray. An Australian species treated as *Clanculus clanguloides* (W. Wood, 1828) (Wilson, 1993: 84). NHMUK 1984191, 4 syntypes.

***clangulus, Trochus** – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 31. Loc.: unknown; Gray. An Australian species treated as *Clanculus clangulus* (W. Wood, 1828) (Wilson, 1993: 85). NHMUK 1884.12.30.1, holotype.

***clelandi, Trochus** – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 15; 56, as *T. clelandii*. Loc.: Ireland; Gray. A northeastern Atlantic and Mediterranean species placed in *Cantharidus* by Fretter & Graham (1977: 72). Type species of the subgenus *Clelandella* Winckworth, 1932. NHMUK 20040854, holotype.

***concameratus, Trochus** – W. Wood, 1828b: 17, pl. 6, *Trochus* fig. 35; 44, as *Monodonta concamerata*. Loc.: unknown; Gray. A southern Australian species treated as *Austrocochlea concamerata* (W. Wood) (Wilson, 1993: 75) and more recently as *Diloma concamerata* (W. Wood) by Donald et al. (2005: 482). NHMUK 196879, 2 syntypes.

***elegantulus, Trochus** – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 9. Loc.: Ceylon; NHMUK. Type species of the subgenus *Praecia* Gray, 1857. NHMUK 1968674, figured by Kaicher (1979: 2086), syntype; NHMUK 20100589, 2 additional specimens from the Gray collection located during the present study, syntypes.

elongatus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 19. Loc.: unknown; NHMUK. *Non Trochus elongatus* J. Sowerby, 1818. Placed in synonymy of the Australian *Thalotia attenuata* (Jonas, 1844) by Wilson (1993: 83). Type material not located in NHMUK in 2010.

filosus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 23. Loc.: unknown; NHMUK. *Non T. filosus* Helbling, 1779. From the Pacific coast of North America. Long recognized as a synonym of *Trochus costatus* Martyn, 1784, and later of *T. ligatus* Gould, 1849 (Pilsbry, 1889: 362) when Martyn's work was declared non-binominal. Figured as *Calliostoma ligatum* (Gould) by Abbott & Dance (1982: 37). NHMUK 20100602, 2 syntypes.

***formosus, Trochus** – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 29; 51 as *Rotella*. Loc.: unknown; Gray. Placed, with a query, in synonymy of the Japanese *Camita rotellina* (Gould, 1849) by Pilsbry (1889: 465), a species that does not attain the size indicated by Wood. Listed by Hanley (1856b: 220) as a synonym of the Japanese *Rotella suturale* (Lamarck, 1822), a placement with which we agree. Wood's name has disappeared from the literature since Pilsbry's work. Type material not located in NHMUK in 2010.

granosus, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 11. Loc.: unknown; NHMUK. *Non Trochus granosus* Lamarck, 1822. This Wood name has disappeared from the subsequent literature. The type appears to be a *Tecturus*, possibly *T. triserialis* (Lamarck, 1822) (S. Williams, personal communication, 9 July 2010). NHMUK 20100603, holotype.

***indistinctus, Trochus** – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 41. Loc.: unknown; Gray. An Australian species from southern Queensland and New South Wales, treated as *Calthalotia indistincta* (W. Wood) (Wilson, 1993: 81). Type material not located in NHMUK in 2010.

interruptus, Trochus – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 42. Loc.: Ireland; Gray. Forbes & Hanley (1850: 2: 505) placed Wood's name at the end of a long series of synonyms of *Trochus exasperatus* Pennant, 1799, a name evidently not previously in use. Their use of this Pennant name must have been a late decision as the plate legend is "*T. exiguus*." *Trochus exiguus* Pulteney, also in the synonymy, was the name in common usage for the British species in question. Forbes

& Hanley described the shell in detail and provided figures that match Wood's in shape, with the coloration and markings also close. The Ireland locality was repeated.

Pilsbry (1889: 358) listed *Trochus interruptus* Wood with locality unknown. He reproduced the figure from Wood and also a figure from Reeve (1863: pl. 8, fig. 64; as *Zizyphinus interruptus*), stating that Reeve is the only author to have identified the species. However, Reeve's figure is not a good match for the one given by Wood, and on the same page Reeve had also placed *interruptus* in the synonymy of *Zizyphinus exiguus* Pulteney, 1799. Melvill & Standen (1898: 77) reported *interruptus* from Madras (as a *Calliostoma*), stating that they had identified it "by Reeve's figure and description, not having seen any named individuals." Kaicher (1979: 2117) figured a specimen stated to be from Ireland "from the NHMUK type collection" that "may be a syntype". It does not match Wood's figure very well and agrees with Reeve's figure of *Z. exiguus*. Subba Rao (2003: 84, pl. 7, fig. 8) illustrated a shell as *Cantharidus interruptus* (Wood, 1856 [sic]) that is neither the species figured by Kaicher nor that of Wood. A survey of published figures of similar taxa offers no solution. It is here considered that Wood's *Trochus interruptus* must be considered a *nomen inquirendum* for the present.

NHMUK 1968707, 2 syntypes representing two species, one a *Jububinus* and the other a calliostomatid. The first is closest to Wood's figure.

listeri, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 8; 44, as *Monodonta*. Loc.: unknown; NHMUK. *Non Trochus listeri* Stewart, 1802. The uncertain identity of this species, and the failure to locate type material, was discussed by Watson (1886: 66), who placed it in the synonymy of *T. colubrinus* Gould, 1849. Indeed, it seems closest to *Osilinus edulis* (Linnaeus, 1758), now considered a senior synonym of *T. columbrinus* (S. Williams, 8 July 2010), from eastern Atlantic islands, Spain, and Senegal. Type material not located in NHMUK in 2010.

maugeri, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 27. Loc.: unknown; NHMUK. An Australian species now treated as *Clanculus maugeri* (W. Wood) (Wilson, 1993: 87). NHMUK 1968614, holotype.

mediterraneus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 32. Loc.: Mediterranean; Gray. Placed in synonymy of the Mediterranean *Trochus cruciatus* Linnaeus, 1758, by Pilsbry (1889: 74) and subsequent workers, a species now considered to belong in *Clanculus*. NHMUK 20100596, 10 syntypes.

montagui, Trochus – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 43. Loc.: Ireland; Gray. This northeastern Atlantic and Mediterranean species placed in the genus *Cantharidus* by Fretter & Graham (1977: 69). See also under *montacuti* below. NHMUK 1968623, 5 syntypes.

obscurus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 26; 44, as *Monodonta*. Loc.: unknown (designated as Durban Bay, South Africa by Herbert, 1994: 139); NHMUK. Type species of both *Priotrochus* P. Fischer, 1879, and its objective junior synonym *Aphanotrochus* Martens, 1880. NHMUK 1992178/1–4, lectotype, 3 paralectotypes (Herbert, 1994: 139–140).

odontis, Trochus – W. Wood, 1828b: 17, pl. 6, *Trochus* fig. 37; 44 as *Monodonta*. Loc.: unknown; Gray. A southern Australian species treated as *Austrocochlea odontis* (W. Wood) by Wilson (1993: 75) and more recently as *Chlorodiloma odontis* (W. Wood) by Donald et al. (2005: 482–483). NHMUK 1968624, 2 syntypes.

pellisserpentis, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 4, as "*pellis serpentis*". Loc.: Panama; Mrs. Mawe. Senior synonym of *Trochus elegans* Lesson, 1832, which is the type species of *Tegula*. *Tegula pellisserpentis* (W. Wood, 1828) occurs from El Salvador to Colombia (Keen, 1971: 337).

pictus, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 28. Loc.: unknown; NHMUK. An Australian species, placed in synonymy of *Thalotia conica* (Gray, 1827) by Wilson (1993: 83). NHMUK 20100594, 2 syntypes found in present study.

pulcherrimus, Trochus – W. Wood, 1828b: 18, pl. 6, *Trochus* fig. 45; 44, as *Monodonta*. Loc.: unknown; Gray. An Australian species now treated as *Cantharidus pulcherrimus* (W. Wood, 1828) (Wilson, 1993: 80). NHMUK 1843.11.24.52, holotype.

quadricostatus, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 16. Loc.: unknown; NHMUK. Recent from northern Peru to Chile and Pleistocene of southern Peru (DeVries, 2007: 171). Type species of the genus *Cantallocostoma* DeVries, 2007. NHMUK 20100604, 5 syntypes.

reticularis, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 21; 44, as *Monodonta*. Loc.: unknown; NHMUK. This species was from New Zealand and was placed in the synonymy of *Monodonta aethiops* (Gmelin, 1791) by Pilsbry (1889: 99), who attributed it to Gray. *Melagraphia aethiops* (Gmelin) (Powell, 1979: 53), is now placed in *Diloma* (Donald et al., 2005: 482). NHMUK 20100615, 3 syntypes.

reticulatus, Trochus – W. Wood, 1828b: 17, pl. 6, *Trochus* fig. 38. Loc.: unknown; Gray. *Non T. reticulatus* J. Sowerby, 1821. This is the Panamic *Tegula verrucosa* McLean, 1970 (pp. 122–123). Described as a new species because of this homonymy, not as a replacement name (see also Keen, 1971: 342). NHMUK 1968712, 3 syntypes.

****smithii, Trochus*** – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 20. Loc.: unknown; NHMUK. A Japanese species, treated as *Monilea smithii* (W. Wood, 1828) by Higo et al. (1999: 67, as *M. "smithi"*). Type material not located in NHMUK in 2010.

sulcatus, Trochus – W. Wood, 1828b: 17, pl. 6, *Trochus* fig. 40. Loc.: unknown; Gray. *Non Trochus sulcatus* Lamarck, 1804, and others. Hanley (1856b: 221) listed it as of Gray with the location as New Zealand but gave no other references or synonyms. Placed in the synonymy of the New Zealand *Monodonta lugubris* (Gmelin, 1791) by Pilsbry (1889: 100), and the latter has been listed as a synonym of *Melagraphia aethiops* (Gmelin, 1791) (Powell, 1979: 53), a species now placed in *Diloma* (Donald et al., 2005: 482). Probably due to being preoccupied, Wood's *sulcatus* has disappeared from synonymies. We cannot identify it with any other taxon with certainty. NHMUK 1968706, 2 syntypes.

trochlea, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 24; 44, as *Monodonta*. Loc.: unknown; NHMUK. *Non Trochus trochlea* Röding, 1798. Placed in synonymy of *Monodonta constricta* Lamarck, 1822, by Hanley (1856: 220), a southern Australian species placed in the genus *Austrocochlea* by Wilson (1993: 75) and Donald et al. (2005: 482). NHMUK 20100605, 4 syntypes.

viridis, Trochus – W. Wood, 1828b: 17, pl. 6, *Trochus* fig. 36; 44, as *Monodonta*. Loc.: unknown; Gray. *Non Trochus viridis* Gmelin, 1791. Stated to be a synonym of the South Australian *T. concameratus* W. Wood, 1828, by Pilsbry (1889: 99), which is now placed in *Diloma* (see above under *concameratus*). NHMUK 1968705, holotype.

zebra, Trochus – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 18; 44, as *Monodonta*. Loc.: unknown; Gray. *Non Trochus zebra* Perry, 1811. Placed in synonymy of *Monodonta fragaroides* Lamarck, 1822, by Hanley (1856b: 220), in turn a synonym of *M. turbinata* (Born, 1778). Mentioned by Bucquoy et al. (1885: 404) as a color form of the Mediterranean *M. turbinata* (Born), which is now placed in the genus *Osilinus*. NHMUK 1968704, holotype.

****zonatus, Trochus*** – W. Wood, 1828b: 17, pl. 5, *Trochus* fig. 34. Loc.: unknown; Gray. A South African species, placed in the genus *Gibbula* by Barnard (1963: 271). NHMUK 20100600, 13 syntypes found in present study.

albus, Trochus – "W. Wood" – Reeve (1863: text to *Zizyphinus* pl. 3) listed this name in the synonymy of *Zizyphinus conuloides* (Lamarck, 1822), without comment. *Nomen nudum*.

articulatus, Trochus – "W. Wood", 1828b: 17, pl. 5, *Trochus* fig. 22. Loc.: unknown; NHMUK. Probably intended to represent *Monodonta articulatus* Lamarck, 1822. Wood's figure was thought by Hanley (1856b: 220) to instead be a specimen of *Trochus villanus* Philippi, 1846, a West African species usually placed in *Clanculus*, but this synonymy seems unlikely.

caerulescens, Trochus – "W. Wood", 1818: 140. – This is *T. caerulescens* Lamarck, 1816, based on the same *Encyclopédie Méthodique* figure.

dentata, Turbo – "W. Wood", 1825: 147. Error by Sherborn (1925: 1847) for *Turbo dentatus*. This name was first made available as *Turbo dentatus* Gmelin, 1791.

laevis, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 13. This was probably intended to be *Trochus laevis* Dillwyn, 1817.

lubeo, Trochus – "W. Wood", 1818: 138 & 1825: 138, with reference to Gmelin (1891: 3578). Error for *T. labio* Linnaeus, 1758. Changed to *labeo* by Wood (1828a:138) and thus never fully corrected, not even by Hanley (1856b: 145).

montacuti, Trochus – "W. Wood" – Jeffreys (1839: 35) introduced this *nomen nudum* as a "new species" but without a description. It was later confounded with *T. montagui* Wood and then attributed to Wood by many authors. It still appears, attributed to Wood, in the synonymy of Wood's taxon (e.g., Fretter & Graham, 1977: 69).

nodulosus, Turbo – "W. Wood", 1818: 147. This is *Turbo nodulosus* Dillwyn, 1817: 843.

taeniatus, Trochus – "W. Wood", 1828b: 16, 56, pl. 5, *Trochus* fig. 12. Name first made available as *Turbo taeniatus* G. B. Sowerby I, 1825 (pp. 55, xiii) (Hanley, 1856b: 219). The Magellanic *Photinula taeniata* (G. B. Sowerby I, 1825) and type species of *Photinastoma* Powell, 1951. This species was misattributed to "Wood, 1825" by Forcelli (2000: 63). Oddly, Pilsbry (1888: 287) had the authorship correct, then later (Pilsbry, 1889: 278) attributed it to Wood.

turbinatus, Trochus – "W. Wood", 1818: 139. Name first made available as *Trochus turbinatus* Born, 1778.

STOMATELLIDAE

imbricata, Haliotis – "W. Wood", 1818: 176; 1828b: 26, pl. 8, fig. 4; 53, as *Stomatella*. This is *Stomatella imbricata* Lamarck, 1816.

phyanotis, Haliotis – "W. Wood", 1818: 176. A spelling error for *Stomatia phymotis* Helbling, 1779, a well-known southwestern Pacific species.

planulata, Haliotis – "W. Wood", 1818: 176. This is *Stomatella planulata* Lamarck, 1816.

sulcifera, Haliotis – W. Wood, 1828b: 26, pl. 8, *Haliotis* fig. 3; 53, as *Stomatella*. This is *Stomatella sulcifera* Lamarck, 1822.

TURBINIDAE

crassus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 43. Loc.: unknown; Mrs. Mawe. *Turbo crassus* Wood occurs from the central Pacific to the southwestern Pacific. (Abbott & Dance, 1982: 47, as "1829").

fluctuosus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 44. Loc.: unknown; Mrs. Mawe. The Panamic *Turbo* (*Callopoma*) *fluctuosus* W. Wood, 1828 (Keen, 1971: 352).

niger, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 1. Loc.: unknown; NHMUK. The Chilean *Prisogaster niger* (W. Wood, 1828) (Forcelli, 2000: 64). Type material not located in NHMUK in 2010.

olivaceus, Trochus – W. Wood, 1828b: 16, 56; pl. 5, *Trochus* fig. 3. Loc.: S[outh] Sea; Mrs. Mawe. The Panamic *Astraea* (*Uvanilla*) *olivaceus* (W. Wood, 1828) (Keen, 1971: 356). *Uvanilla* is now treated as a full genus (S. Williams, personal communication, 5 July 2010).

saxosus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 45. Loc.: unknown; Mrs. Mawe. The Panamic *Turbo* (*Callopoma*) *saxosus* W. Wood, 1828 (Keen, 1971: 352).

undosus, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 1. Loc.: California; Mrs. Mawe. The Californian *Astraea* (*Megastraea*) *undosus* (W. Wood, 1828) (McLean, 1978: 24). Type species of *Megastrea* McLean, 1970, which is now treated as a full genus (S. Williams, personal communication, 5 July 2010).

unguis, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 2. Loc.: unknown; Mrs. Mawe. The Panamic *Astraea* (*Uvanilla*) *unguis* (W. Wood, 1828) (Keen, 1971: 356). *Uvanilla* is now treated as a full genus (S. Williams, personal communication, 5 July 2010).

ludus, Turbo – "W. Wood", 1818: 154. This is *Turbo ludus* Gmelin, 1791, now considered a junior synonym of *Turbo undulatus* Lightfoot, 1786. This Australian species, figured by Abbott & Dance (1982: 48) as *Subninella undulata* (Lightfoot, 1786), is now placed in *Lunella* (S. Williams, personal communication, 5 July 2010).

PHASIANELLIDAE

lineolatus, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 26; 48, as *Phasianella*. Loc.: Isle of France [Mauritius]; Gray. Synonym of the Indo-Pacific *Phasianella variegata* Lamarck, 1822 (Pilsbry, 1888: 179). The latter is a junior primary homonym, *non* Roissy, 1805, and the name *P. rubens* Lamarck, 1822, has been used for this species (Robertson, 1958: 256, footnote). NHMUK 1963302, 8 syntypes.

perdix, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 46; 48, as *Phasianella*. Loc.: unknown; Mrs. Mawe. Placed in synonymy of the Australian *Phasianella ventricosa* Swainson, 1822, by Wilson (1993: 1: 102).

varius, Turbo – "W. Wood", 1828b: 19, pl. 6, fig. 25. This is *Phasianella varia* Lamarck, 1816, a synonym of the Australian *Phasianella australis* (Gmelin, 1791).

HELICINIDAE

scitula, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 64; 39, as *Helicina*. Loc.: W. Indies; NHMUK. A Jamaican species, treated as *Eutrochatella pulchella scitula* (W. Wood, 1828) by Rosenberg & Muratov (2006: 142). Type material not located in NHMUK in 2010.

aureola, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 65; 39, as *Helicina*. Name first made available as *Helicina aureola* Gray, 1824. Now *Lucidella aureola* (Gray, 1824) (Rosenberg & Muratov, 2006: 142).

brownii, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 63; 39, as *Helicina*. Name first made available as *Helicina brownii* Gray, 1824. Now *Alcadia brownii* (Gray, 1824) (Rosenberg & Muratov, 2006: 141).

tankervillii, Trochus – "W. Wood", 1828b: 16, pl. 5, *Trochus* fig. 10. Name first made available as *Helicina tankervillii* Gray, 1824, from Jamaica (Hanley, 1856: 219). Now *Eutrochatella tankervillii* (Gray, 1824) (Abbott, 1989: 33; Rosenberg & Muratov, 2006: 142).

NERITIDAE

australis, Nerita – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 5. Loc.: New Holland; NHMUK. *Non Nerita australis* Gmelin, 1791. Long recognized as a synonym of *Nerita antiquata* Récluz, 1841, which is now treated as a subspecies of *Nerita polita* Linnaeus, 1758 (Abbott & Dance, 1982: 53). Type material not located in NHMUK in 2010.

caffra, Nerita – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 10; 45, as *Neritina*. Loc.: Africa; Gray. Placed in the synonymy of *Neritina gagates* Lamarck, 1822, by Morelet (1875: 29), where it remains (Fischer-Piette & Vukadinovic, 1973: 342). This freshwater snail occurs from South Africa to Madagascar and the Seychelles. Type material not located in NHMUK in 2010.

****cariosa, Nerita*** – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 9; 45, as *Neritina*. Loc.: "Africa"; Gray. The stated locality was incorrect. This brackish-water species is endemic to Hawaii (Kay, 1979: 66) as *Theodoxus cariosus* (W. Wood, 1828). Type of the subgenus *Alinoclithon* Baker, 1923. NHMUK 196574–75, 3 syntypes.

****oweniana, Nerita*** – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 8; 45, as *Neritina*. Loc.: Africa; Donovan [sic; error for Gray]. This freshwater snail treated as *Neritina oweniana* (W. Wood, 1828) by Brown (1980: 40), who gave its distribution as Liberia to Angola. See *N. owenii* below. NHMUK 20100593, 9 syntypes (2 large, 7 small) found in present study.

owenii, Nerita – W. Wood, 1828b: 26, pl. 8, *Nerita* fig. 16; 45, as *Neritina* [cited there in error as being "fig. 17"]. Loc.: Africa; Mrs. Mawe. The history and status of this name is confused. Germain (1908: 111) listed it as "*Neritina oweni* [sic] Gray" from Cameroon and adjacent areas. The name "*oweni*" does not appear in Germain's chresonymy, the first item of which is "1828. *Neritina oweniana* Gray in Wood". Dall (1909: 241) listed "*Neritina owenii* Mawe", with reference to Wood (1828b), from "Costa Rica, and south to Paita, Peru." It is not in Keen (1971), but listed as a Peruvian species by Ramirez et al. (2003: 259), who probably just repeated Dall as they attributed the name to Mawe. Gray (1831: 11) treated *Neritina owenii*, his references being, "*Nerita oweniana* Gray. Wood, Cat. Suppl. t. 8, f. 8, and *N. owenii*, f. 16? imperfect." The name has not been located elsewhere, and we accept Gray's synonymy of *owenii* with *oweniana*.

pulchella, Nerita – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 18; 45, as *Neritina*. Loc.: W. Indies; NHMUK. Stated to be a synonym of *N. meleagris* Lamarck, 1822, by Hanley (1856b: 232), it has remained there. This species was transferred to the genus *Theodoxus* by Baker (1923: 157), who gave its distribution as South Carolina, Bermuda and Mexico to Brazil. Type material not located in NHMUK in 2010.

rudis, Nerita – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 13. Loc.: Africa; Gray. Placed in synonymy of the African *Nerita* (*Theliostyla*) *reticulata* Karsten, 1789, by Adam & Leloup (1938: 52). Type material not located in NHMUK in 2010.

****smithii, Nerita*** – W. Wood, 1828b: 25, pl. 8, *Nerita* fig. 11; 45 as *Neritina*. Loc.: Africa; Gray. Original locality incorrect; given as an estuarine species occurring from India to Tahiti by Baker (1923: 145), who made it the type species of his subgenus *Provittoida*. NHMUK 1990072, 7 syntypes.

auriculata, Nerita – "W. Wood", 1818: 174. This is *Neritina auriculata* Lamarck, 1816, now placed in the genus *Clypeolum.*

canalis, Nerita – "W. Wood", 1828b: 26, pl. 8, *Nerita* fig. 17. This is *Neritina canalis* G. B. Sowerby I, 1825.

crepidularia, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 6; 45, as *Neritina*. This is *Neritina crepidularia* Lamarck, 1822.

ornata, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 4. This is *Nerita ornata* G. B. Sowerby I, 1823.

semiconica, Nerita – "W. Wood", 1828b: 26, pl. 8, *Nerita* fig. 15. This is *Neritina semiconica* Lamarck, 1822.

spinosa, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 12; 45, as *Neritina.* Names first made available as *Neritina spinosa* G. B. Sowerby I, 1825, which was placed in synonymy of *Theodoxus* (*Clithon*) *corona* (Linnaeus, 1758) by Adam & Leloup (1938: 58).

AMPULLARIIDAE

conica, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 22; 29, as *Ampullaria*. This was probably intended to represent *Ampullaria conica* Swainson, 1823, which is *non* Lamarck, 1804 [Naticidae]. Cowie (1997: 3, 4) listed *Ampullaria conica* Wood, 1828, under the genus *Pila*, as a Hawaiian Islands pest with a range through eastern Asia. Cowie considered *Ampullaria conica* to be "the original combination", contrary to the current treatment of Wood's taxa. It is immaterial in this instance, because *conica* is preoccupied numerous times in both *Ampullaria* and *Helix*. Some of these homonyms were discussed by Cowie & Thiengo (2003: 52). Cowie advises (personal communication, 8 February 2010) that there are several junior subjective synonyms available for this species, but that he is still studying the problem.

CYCLOPHORIDAE

laevis, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 5; 36, as *Cyclostoma*. Loc.: unknown; NHMUK. Junior synonym of *Leptopoma marginellum* (Gmelin, 1791) (Pfeiffer, 1852a: 74; 1852b: 105; who listed both under the unavailable name *L. immaculata* Chemnitz). This Philippine species is type of the genus *Leptotoma* Pfeiffer, 1847. Type material not located in NHMUK in 2010.

petiverianus, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 2; 36, as *Cyclostoma*. Loc.: unknown; NHMUK. The Malayasian *Myxostoma petiverianum* (W. Wood, 1828), the type and sole species of its genus (Abbott, 1989: 38). Type material not located in NHMUK in 2010.

foliaceus, Turbo – "W. Wood", 1818: 151. Name first made available as *Turbo foliaceus* Gmelin, 1791.

lunulatus, Turbo – "W. Wood", 1818: 150. Name first made available as *Turbo lunulatus* Gmelin, 1791.

marginellus, Turbo – "W. Wood", 1818: 154. Name first made available as *Turbo marginellus* Gmelin, 1791.

oculuscapri, Cyclophorus – "Wood", 1828a: 155. – Pfeiffer (1852b: 87). Attributed to Wood with a long synonymy, although the name was introduced by Linnaeus (1758) and cited by Gmelin (1791), the latter reference being cited in turn by Wood. Pfeiffer cited Wood's plate 32, *Helix* figure 7, as the basis for the name. The treatment of *Cyclostoma oculuscapri* Wood by Petit (2007: 56) is incorrect in attributing the species to Wood. Even if it is a misidentification by Wood, the name cannot be attributed to him.

Pfeiffer (1852b) listed both *Cyclophorus involvulus* and *C. oculuscapri* as species and referenced Wood's plate 32, fig. 7, for both. In Wood (1828a), figure 7 is denoted as *Helix oculuscapri* and "figure 8" as *H. involvulus*. The latter to both Gmelin and Müller. In his introduction, Wood pointed out that some figures had been skipped as they had not been figured by their authors and he did not have specimens available from which to make drawings. Such was the case with *H. involvulus*, and there is no figure 8 on plate 32. Pfeiffer (1852a: 38–39) treated *Cyphophorus volvulus* (Müller) and *C. involvulus* (Müller) consecutively, listing Wood's usage of *volvulus* only under the latter. Pfeiffer (1852a: 60–61) treated *C. oculuscapri*, attributed to Linnaeus with *Helix oculuscapri* Wood, 1828a, pl. 32, fig. 7, in synonymy.

Abbott (1989: 38) figured *Cyclophorus involutus* [sic] (Müller, 1774) from Sri Lanka. The status of the other taxa involved has not been determined, and we are unable to offer more information on the identification of the two species involved, but we trust determining their status will provide some land snail systematist with many hours of amusement.

planorbula, Helix – "W. Wood", 1818: 157. This is *Cyclostoma planorbula* Lamarck, 1816.

valvulus, Cyclostoma – "W. Wood", 1828b: 36; ref. to 1828a, pl. 32, fig. 7. There (1828a: 155) the figure is labeled as *Helix oculuscapri*, with references to Gmelin, Lister and Chemnitz. Possibly a typographical error by Wood for *involvulus*, which was the next species figured. However, Hanley (1856b: 163) continued to list figure 7 as *oculus-capri* and stated that "It is neither Lin. Sys. nor Müll." but is *C. variegatus* Philipi, 1844. See *oculuscapri* above.

volvulus, Helix – "W. Wood" – Pfeiffer (1852a: 39; 1852b: 60) in reference to Wood's plate 32, figure 7, in the synonymy of *Cyclophorus involvulus* (Müller). The spelling *volvulus* does not appear in either Wood 1828a or 1828b.

ACICULIDAE

fuscus, Turbo – "W. Wood", 1828b:19, pl. 6, *Turbo* fig. 15; 47, as *Paludina*. This is *Turbo fuscus* Montagu, 1803, which is now placed in the genus *Acicula*.

DIPLOMMATINIDAE

maculatus, Turbo – "W. Wood", 1828b: 19, pl. 6, *Turbo* fig. 11; 36, as *Cyclostoma*. Name first made available as *Cyclostoma maculatum* Draparnaud, 1805.

MEGALOMASTOMATIDAE

flavidus, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 31; 36, as *Cyclostoma*. Loc.: unknown; Gray. Identified by Hanley (1856b: 224) as *Cyclostoma flavulum* Lamarck, 1816, a species that Petit de la Saussaye (1850: 45) and others placed, together with Wood's species, in the synonymy of *Cyclostoma croceum* (Gmelin, 1791). Wood's name has disappeared from the literature. This Jamaican species has been treated by Abbott & Dance (1989: 45) as *Megalomostoma croceum* (Gmelin, 1791). Type material not located in NHMUK in 2010.

****tortus, Turbo*** – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 32; 36, as *Cyclostoma*. Loc.: unknown; Gray. A Cuban land snail now placed in *Farcimen* (Abbott, 1989: 44). Type material not located in NHMUK in 2010.

NEOCYCLOTIDAE

jamaicensis, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 3; 36, as *Cyclostoma*. Loc.: West Indies; NHMUK. The Jamaican type species of *Poteria* Gray, 1840; *P. jamaicensis* (W. Wood, 1828) (Abbott, 1989: 43). However, this is *Turbo jamaicensis* Dillwyn, 1823 (Rosenberg & Muratov, 2006: 146). Type material not located in NHMUK in 2010.

VIVIPARIDAE

decisa, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 17; 47, as *Paludina*. Loc.: freshwater of North America; Wood collection. *Non Paludina decisa* Say, 1819. Placed in synonymy of *Lioplax subcarinata* (Say, 1819) by Hanley (1856b: 226) and Tryon (1870: 52), where it remains.

dissimilis, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 18; 47, as *Paludina*. Loc.: freshwater of North America; Wood collection. Placed in synonymy of *Vivipara decisa* (Say, 1817) by Green (1830: 135), Hanley (1856b: 226), and Tryon (1870: 52). Now *Campeloma decisum* (Say, 1817) (Turgeon et al., 1998: 63).

funis, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 48. Loc.: unknown; Mrs. Mawe. Placed in the synonymy of *Paludina bicolor* G. B. Sowerby I, 1825, by Hanley (1856b: 225) with a query. Type material not located in NHMUK in 2010.

subcarinata, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 13; 47, as *Paludina*. Loc.: freshwater, N. America; "L. T. 13, pl. 5, fig. 1". This is *Lioplax subcarinatus* (Say, 1816). However, the figure cited in the *Linnean Transactions* is *Helix angulata* Rackett, 1821, corresponding to Wood's figure 12.

CERITHIIDAE

curvirostris, Murex – W. Wood, 1818: 131. Loc.: Amboyna. Wood referred to Chemnitz (1780: pl. 156, fig. "1748" [sic; =1478]), a figure of the Indo-Pacific *Pseudovertagus aluco* (Linnaeus, 1758). Houbrick (1978: 101–105) discussed the latter and its synonyms, but not Wood's taxon. This is neither *Cerithium curvirostra* Perry, 1811 (a synonym of *Cerithium nodulosum* Bruguière, 1892), nor *Murex curvirostris* W. Wood, 1828b (see under Buccinidae).

exasperatus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 21; 34, as *Cerithium exasperatum*. Loc.: unknown; Mrs. Mawe. Stated by Hanley (1856b: 218) to be a synonym of *Cerithium echinatum* Lamarck, 1822, and apparently absent from subsequent literature. The Indo-Pacific *C. echinatum* Lamarck was treated by Wilson (1993: 117).

****petrosus, Strombus*** – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 9; 34, as *Cerithium*. Loc.: East Indies; Mrs. Mawe. An Indo-Pacific species treated as *Clypeomorus petrosa* (W. Wood) by Houbrick (1985: 69–77). NHMUK 1985084, possible holotype, located in present study.

pictus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 24; 34, as *Cerithium mitriforme* in error; 44, with reference to fig. 23 in error. Loc.: unknown; Mrs. Mawe. *Non Cerithium pictum* Basterot, 1825. Wood's species, which occurs both in West Africa and the Caribbean, was placed in the synonymy of *Cerithium guinaucum* Philippi, 1849, by Houbrick (1974: 67–71).

rugosus, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 10; 34, as *Cerithium*. Loc.: unknown; NHMUK. *Non Strombus rugosus* Lamarck, 1804. An Indo-Pacific species placed in the synonymy of *Clypeomorus brevis* (Quoy & Gaimard, 1834) by Houbrick (1985: 43–50). NHMUK 1985083, holotype.

****zonatus, Strombus*** – W. Wood, 1828b: 13, pl. 4, fig. 7; 34, as *Cerithium*. Loc.: unknown; Mrs. Mawe. An Indo-Pacific species treated by Houbrick (1992: 193) as *Cerithium zonatum* (W. Wood, 1828). Because type material could not be located, Houbrick designated USNM 862843 from Bandicoot Bay, Barrow Id., Western Australia as a neotype.

granulatus, Murex – "W. Wood", 1818: 132. This name was used by Dillwyn, 1817, who cited same Chemnitz figures as Wood. Bruguière (1792) also cited the same Chemnitz figures for his *Cerithium granulatum*. The status of this taxon appears to be unresolved. For discussions, see Houbrick (1978: 38–41) and Dodge (1957: 201–204).

mitriforme, Cerithium – "W. Wood", 1828b: 34. Wood mistakenly inserted this name when he meant to list *Cerithium pictum* (see above).

obeliscus, Murex – "W. Wood", 1825 & 1828a: 131, pl. 27, fig. 142. Listed in synonymy of *Rhinoclavis sinensis* (Gmelin, 1791) by Houbrick (1978: 56). Wood used the same species name as Bruguière and also, in parentheses, cited Gmelin's *sinensis*. This is thus merely *Cerithium obeliscus* Bruguière, 1792, and not attributable to Wood.

obtusus, Strombus – "W. Wood", 1828b: 13, pl. 4, *Strombus* fig. 8; 34, as *Cerithium*. The Indo-Pacific *Cerithium obtusum* Lamarck, 1822.

semi-granosus, Murex – "W. Wood", 1818: 132. Name first made available as *Cerithium semigranosus* Lamarck, 1816 (*non* Lamarck, 1804), based on the same figure in the *Encyclopédie Méthodique*. This Indo-Pacific species is now known as *Rhinoclavis bituberculata* (G. B. Sowerby II, 1866) (Houbrick, 1978: 63).

serratum, Murex – "W. Wood", 1825 & 1828a: 132, pl. 28, fig. 158. This was intended to be *Cerithium serratum* Bruguière, 1792. Both Schepman (1909: 159) and Houbrick (1978: 72) attributed this name to Wood.

MELANOPSIDAE

melanopsis, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 27. Loc.: S. of Europe; Gray. Recognized by Hanley (1856b: 214) as being *Melanopsis costata* (Oliver, 1804) [originally described in *Melania*], a freshwater species from the Levant. Wood changed the species name when he placed it in the Linnaean *Buccinum*, because there was already a *B. costatum* Linnaeus, 1758. Wood's name has disappeared from the literature and is not listed in recent synonymies (e.g., Heller et al., 2002: 596). Type material not located in NHMUK in 2010.

PLEUROCERIDAE

sayii, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* fig. 24; 42, as *Melania*. Loc.: N. America; NHMUK. Stated by Green (1830: 136) to be a renaming by Gray of *M. canaliculata* Say because it was preoccupied, but we cannot find an earlier use of this name. Placed in the synonymy of the Ohio River *Pleurocera canaliculatus* (Say, 1821) by Goodrich (1929: 10). Misspelled as *sayi* by Sherborn (1930: 5764). Type material not located in NHMUK in 2010.

fluviatilis, Helix – "W. Wood", 1818: 167. This is *Helix fluviatilis* Dillwyn, 1817, which = *Helix lanschaurica* Gmelin, 1791, all these based on same Chemnitz figure.

virginea, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 19. Loc. N. America, freshwater; Wood's collection. A spelling error for the name first made available as *Melania virginica* Say, 1817. Now *Elimia virginica* (Say, 1817) (Turgeon et al., 1998: 67).

PLANAXIDAE

laevigatum, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 29; 49, as *Planaxis*. Loc.: unknown; Gray. *Non B. laevigatum* Linnaeus, 1758. Synonym of *Planaxis mollis* G. B. Sowerby I, 1823, which in turn is now regarded as a synonym of the southeastern Pacific *Hinea brasiliana* (Lamarck, 1822) (Abbott & Dance, 1982: 62). Type material not located in NHMUK in 2010.

planaxis, Buccinum – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 15; 49, as *Planaxis*. Loc.: unknown; Mrs. Mawe. Synonym of the Panamic-Pacific *Planaxis planicostatus* G. B. Sowerby I, 1825 (Keen, 1971: 417).

THIARIDAE

****byronensis, Strombus*** – Wood, 1828b: 14, pl. 4, *Strombus* fig. 23; 42, as *Melania*. Loc.:

S. Amer.; NHMUK. Treated as *Pachymelania byronensis* (W. Wood, 1828) by Brown (1980: 112), who cited the type locality as Upper Guinea and gave a distribution from Ivory Coast to Nigeria. Type material not located in NHMUK in 2010.

lineata, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 68; 42, as *Melania*. Loc.: "East Indies"; NHMUK. *Non Helix lineata* Say, 1821. Synonym of *Melania lirata* Benson, 1830 (Brot, 1870: 296, who listed Wood's species as "1825", noting that it was a Gray MS name).

lineolatus, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 11; 42, as *Melania*. Loc.: not stated; NHMUK. Jamaican type species of *Hemisinus* Swainson, 1840 (Petit & Coan, 2008: 235). NHMUK 1984206/1–7, lectotype and 6 paralectotypes (Nuttall, 1990: 239–240). Species recently discussed by Gomez et al. (2011).

sulculata, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 73; 42, as *Melania*. Loc.: unknown; Mrs. Mawe. Listed by Brot (1870: 303) under "*Melaniae ignota vel incertae sedis*." No other citations have been located.

auritus, Strombus – "W. Wood", 1828b: 14, pl. 4, *Strombus* fig. 22. The Senegalese *Vibex auritus* (Müller, 1773) (Brot, 1870: 306), originally described in *Nerita*.

bulimoides, Turbo – "W. Wood", 1828b: 19, pl. 6, *Turbo* fig. 27; 47, as *Paludina*. Loc.: Isle of France [Mauritius]; Gray. Listed as synonym of *Cyclostoma bulimoides* Olivier, 1804, by Hanley (1856b: 224), who also cited the placement of Olivier's species in *Paludina* by Deshayes (1838: 517). No recent mentions of Wood's association with this name have been located.

fasciolata, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 72; 42, as *Melania*. This is *Melanoides fasciolata* Olivier, 1804.

laevissima, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 26; 42, as *Melania lineolata* in error. This is *Melania laevissima* G. B. Sowerby I, 1824.

TURRITELLIDAE

turritella, Turbo – W. Wood, 1818: 151. The only reference given was to Lamarck (1816: pl. 449, lower fig. 2), with *Turritella* capitalized in Wood. On Lamarck's plate 449 there are three species of *Turritella*: figure 1a, b was named by Lamarck as *T. duplicata*, and figure 3a, b was identified as *T. terebra* (Linnaeus, 1758). In 1816, Lamarck did not provide a name for figure 2a, b, listing it simply as "*Turritella*." When Lamarck (1822: 57) introduced the name *Turritella cornea*, the 1816 figure 2a, b was the only reference. Thus, *Turbo turritella* Wood, 1818, is a senior objective synonym of *T. cornea* Lamarck, 1822. However, both names seem to be *nomina dubia* and not recognized in recent literature.

CALYPTRAEIDAE

peziza, Patella – W. Wood, 1828b: 26, pl. 8, *Patella* fig. 3. Loc.: unknown. NHMUK. Synonym of the eastern Pacific *Crucibulum spinosum* (G. B. Sowerby I, 1824) (Keen, 1971: 463). Type material not located in NHMUK in 2010.

poculum, Patella – W. Wood, 1828b: 26, pl. 8, *Patella* fig. 2. Loc.: unknown. NHMUK. Synonym of *Calyptraea radians* (Lamarck, 1816) (Hanley, 1856b: 233), which was in turn placed into the synonymy of the eastern Pacific *C.* (*Trochita*) *trochiformis* (Born, 1778) by Keen (1971: 456). Type material not located in NHMUK in 2010.

scutellata, Patella – W. Wood, 1828b: 26, pl. 8, *Patella* fig. 4. Loc.: unknown, NHMUK. The eastern Pacific *Crucibulum scutellatum* (W. Wood, 1828) (Keen, 1971: 463). Type material not located in NHMUK in 2010.

CAPULIDAE

cornu, Argonauta – "W. Wood", 1818: 62. This is *Argonauta cornu* Gmelin, 1791, the South African *Lippistes cornu* (Gmelin, 1791), which was figured by Abbott & Dance (1982: 71).

CYPRAEIDAE

commixta, Cypraea – W. Wood, 1828b: 9, pl. 3, *Cypraea* fig. 11. Loc.: Indian Ocean; Mrs. Mawe. Placed in synonymy of *C. pallidula* Gaskoin, 1849, with a query by Schilder & Schilder (1971: 54). Listed as synonym of *C. interrupta* Gray, 1824 in index of Taylor & Walls (1975: 275). Wood's species has been ignored in later literature.

interstincta, Cypraea – W. Wood, 1828b: 9, pl. 3, *Cypraea* sp. 9. Loc.: unknown; Mrs. Mawe. Currently treated as a subspecies of *C. limacina* Lamarck, 1810 (Taylor & Walls, 1975: 279; Lorenz & Hubert, 2000: 211, 530).

lactea, Cypraea – W. Wood, 1828b: 8, pl. 3, *Cypraea* fig. 2. Loc.: "S[outh] Seas"; Mrs. Mawe. Junior synonym of *Cypraea eburnea* Barnes, 1824 (Barnes, 1885: 217; Taylor & Walls, 1975: 279; Lorenz & Hubert, 2000: 191, 553).

clandestina, Cypraea – "W. Wood", 1828b: 9, pl. 3, *Cypraea* fig. 17. Name first made available by Linnaeus, 1767.

gangraenosa, Cypraea – "W. Wood", 1818: 83. Name first made available as *Cypraea gangranosa* Dillwyn, 1817, which was then misspelled by Wood.

margarita, Cypraea – "W. Wood", 1818: 84. Name first made available by Dillwyn, 1817.

nivea, Cypraea – "W. Wood", 1828b: 9, pl. 3, *Cypraea* fig. 12. Name first made available by Gray, 1824.

quadrimaculata, Cypraea – "W. Wood", 1828b: 9, pl. 3, *Cypraea* fig. 8. Name first made available by Gray, 1824.

tessellata, Cypraea – "W. Wood", 1828b: 8, pl. 3, *Cypraea* fig. 1. Name first made available by Swainson, 1822.

OVULIDAE

imperialis, Bulla – "W. Wood", 1818: 85. Name first made available as *Bulla imperialis* Dillwyn, 1817, a synonym of *Ovula costellata* (Lamarck, 1810).

lepida, Bulla – "W. Wood", 1818: 85. Name first made available by Dillwyn (1817) from same figure cited by Wood; = *Pseudosimnia carnea* (Poiret, 1789).

FICIDAE

decussata, Bulla – W. Wood, 1828b: 9, pl. 3, *Bulla* fig. 3. Loc.: Panama; Mrs. Mawe. Synonym of *Ficus ventricosa* (G. B. Sowerby I, 1825) (Keen, 1971: 503).

LITTORINIDAE

acuminatus, Trochus – W. Wood, 1828b: 16, 56, pl. 5, *Trochus* fig. 6. Loc.: S[outh] Seas; Mrs. Mawe. Wrongly placed in the synonymy of the South African *Trochus capensis* Gmelin, 1791 [now *Gibbula*], by Hanley (1856b: 219). According to Reid (1988: 135–139), this is instead a junior synonym of *Bembicium nanum* (Lamarck, 1822), a trochid-appearing littorinid.

bicarinatus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 47. Loc.: unknown; Mrs. Mawe. *Non Turbo bicarinatus* G. B. Sowerby I, 1825. Wood's species was recognized as Panamic by Mörch (1861: 69). It was attributed to Gray and placed, with a query, in the synonymy of *Littorina varia* G. B. Sowerby I, 1832, by Tryon (1887: 246). However, according to Reid (1999: 38–39), it is more likely *Littoraria variegata* (Souleyet, in Edoux & Souleyet, 1852).

minimus, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 29. Loc.: unknown; Gray. Synonym of the western Atlantic *Echinolittorina mespillum* (Mühlfeld, 1824) (Bequaert, 1943: 21; Abbott, 1974: 68, both as *Littorina*; Reid, 2009: 22–27). NHMUK 1968369, 2 syntypes.

*****pintado, Turbo*** – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 34. Loc.: Sandwich Isl. [Hawaii]; Gray. The Indo-Pacific and Panamic *Littoraria* (*Protolittoraria*) *pintado* (W. Wood, 1828) (Reid, 1986: 73; 1999: 23–32). NHMUK 1968368, 17 syntypes.

rugosus, Trochus – W. Wood, 1828b: 16, pl. 5, *Trochus* fig. 7; 44, as *Monodonta*. Loc.: unknown [Mindanao, Philippines – Rosewater, 1973: 69]; NHMUK. *Non Trochus rugosus* Röding, 1798, and a synonym of the Indo-Pacific *Tectarius coronatus* Valenciennes, 1832 (Rosewater, 1973: 68–69). NHMUK 1968370, "lectotype" (Rosewater, 1973: 69), but specimen received by NHMUK too late to have been present when Wood named the species. NHMUK 20100595, two more likely syntypes, located during the present study.

tuberculatus, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 30. Loc.: E. Indies; Gray. *Non Turbo tuberculatus* Pennant, 1777. Junior subjective synonym of the Caribbean *Tectarius antonii* (Philippi, 1846). This taxon was often confused with *Litorina* [sic] *tuberculata* Menke, 1828, until this species complex was treated by Bandel & Kadolsky (1982). Wood's species was later discussed and placed in *Tectarius* by Reid (2009: 71). NHMUK 1887.4.26.13, lectotype; 14–15, paralectotypes.

zebra, Turbo – W. Wood, 1828b: 13, pl. 6, *Turbo* fig. 33. Loc.: S. America; Gray. *Non Turbo zebra* Donovan, 1825. Recognized by Philippi (1847: 165) and Hanley (1856b: 224) as *Littorina peruviana* (Lamarck, 1822); Philippi gave seniority to Wood, having misdated Wood as 1818 instead of 1828. Figured by Abbott & Dance (1982: 56) as *Littorina peruviana* (Lamarck). Treated as *Nodilittorina peruviana*

(Lamarck) by Reid (2002: 147–149), but still later as *Echinolittorina peruviana* (Lamarck) by Williams & Reid (2004). NHMUK 1968367, 18 syntypes.

foliosum, Buccinum – "W. Wood", 1818, 1825 & 1828a: 106. Spelling error for *B. foliorum* Gmelin, 1791, a synonym of *Littoraria* (*Littorinopsis*) *scabra* (Linnaeus, 1758), which was treated by Reid (1986: 94–96) without reference to Wood's taxon. However, what Wood (1825: pl. 22, fig. 39) figured was instead the European *Nassarius mutabilis* (Linnaeus, 1758). Wood's misspelling was listed by both Tryon (1882: 22) and by Cernohorsky (1984: 51) in the synonymy of the latter.

muricatus, Turbo – "W. Wood", 1818: 143. This is *Turbo muricatus* Linnaeus, 1758.

penitaria, Littorina – "W. Wood". A *nomen nudum* in Nevill (1885: 142).

tuberculata, Littorina – "W. Wood". Sherborn (1931: 6667) listed "*tuberculata, Littorina* (Wood)", based on a citation in Gray (1839: 140), having missed Wood's publication of this species as *Turbo tuberculatus* (see above).

POMATIIDAE

carinatus, Turbo – "W. Wood" – Pfeiffer (1852a: 138; 1852b: 197) listed this as of Wood in the synonymy of *Cyclostomus tricarinatus* (Müller, 1774). However, Wood's (1825 & 1828a: 151, pl. 32, fig. 125) listing was taken from Dillwyn's (1817: 866) treatment of *Turbo carinatus* Born, 1778. Abbott (1989: 48–49) figured several forms of the variable *Tropidophora tricarinatus* (Müller, 1774).

ANNULARIIDAE

aurantius, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 23; 36, as *Cyclostoma*. Loc.: unknown; Gray. Treated by Watters (2006: 157) as *Tudora aurantia* (W. Wood, 1828) ranging through the Netherlands Antilles. Watters reported that the type is in the NHMUK labeled "from Gray Coll. 98.5.11.10", but it was not located in 2010.

chemnitzii, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 6; 36, as *Cyclostoma*. Loc.: unknown, NHMUK. Watters (2006: 200) observed that it is "Unrecognizable from figure. Resembles a *Licina*." He reported that the type could not be located in the NHMUK. NHMUK 20100493, syntype, ex J. E. Gray collection.

columna, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 21; 36, as *Cyclostoma*. Loc.: unknown; Gray. The Jamaican *Parachondria columna* (W. Wood, 1828) (Rosenberg & Muratov, 2006: 148). Type material not located in NHMUK in 2010.

compressus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 42; 36, as *Cyclostoma*. Loc.: unknown; NHMUK. Rosenberg & Muratov (2006:147) listed as a synonym of the Jamaican *Annularia lincina* (Linnaeus, 1758). Watters (2006: 212) did not locate a type specimen in the NHMUK, nor was it located in 2010.

elongatus, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 10; 36, as *Cyclostoma*. Loc.: unknown; NHMUK. Listed by Watters (2006: 247) in his work on Caribbean Annulariidae as a *nomen dubium*. Watters did not locate a type specimen in the NHMUK.

fascia, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 8; 36, as *Cyclostoma*. Loc.: unknown; NHMUK. Listed by Rosenberg & Muratov (2006: 148) as *Parachondria fascius* (W. Wood, 1828), a Jamaican species that is type species of *Parachondria*. Watters (2006: 260) stated that "NHMUK 54.5.19.92–98, labeled 'Jamaica,' collected by Chitty, may be holotype and matches type figure." This, however, was received by the NHMUK too late to be Wood's material. NHMUK 20100495, 5 syntypes on two board, *ex* J. E. Gray collection.

fulvus, Turbo – W. Wood, 1828b:18, pl. 6, *Turbo* fig. 9; 36, as *Cyclostoma*. Loc.: Minorca; NHMUK. Placed in the synonymy of *Cyclostoma ferruginea* Lamarck, 1822, by Forbes & Hanley (1852: 204), Pfeiffer (1852a: 172; 1852b: 245), and Hanley (1856b: 223). Wood's synonym has disappeared from recent literature. *Tudorella ferruginea* (Lamarck, 1822) occurs in Spain's Balearic Isles (Martinez-Orti et al., 2008: 563). NHMUK 20100492, syntype, *ex* J. E. Gray collection.

mirabilis, Turbo – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 22; 36, as *Cyclostoma*. Loc.: unknown; Gray. A Jamaican species treated as *Adamsiella mirabilis* (W. Wood, 1828) by Watters (2006: 356). NHMUK 20100494, 3 syntypes, *ex* J. E. Gray collection.

pulcher, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 4; 36, as *Cyclostoma*. Loc: unknown; NHMUK. A Jamaican species treated by Watters (2006: 421), as *Megannularia pulchra* (W. Wood, 1828). As noted by Petit & Coan (2008: 237), *Cyclostoma pulchra* was incorrectly listed by Sherborn (1929: 5233) as a transfer by Wood of *Turbo pulcher* Dillwyn, 1817. That Wood's taxon is a junior primary homonym but not synonym of *Turbo pulcher* Dillwyn, 1817, has not been noted. Resolution is left to land-snail specialists. Wood's name is also *non Turbo pulcher* Reeve, 1843. Watters did not locate type material in the NHMUK.

elegans, Turbo – "W. Wood", 1818: 150. This is *Turbo elegans* Gmelin, 1791, based on same figures cited by Wood.

lincea, Turbo – "W. Wood", 1818: 150, pl. 31, *Turbo* fig. 119, Spelling error by Sherborn for *Turbo lincina* Linnaeus, 1758, which was spelled correctly by Wood.

NATICIDAE

candida, Nerita – W. Wood, 1818: 169. Loc.: Moluccas. This name was based on figures in Chemnitz (1781: pl. 187, figs. 1887–1891) and Lamarck (1816: pl. 453, fig. 3), the latter figure having been earlier named *Natica chinensis* Lamarck, 1816. Röding (1798: 147) also based two names on the Chemnitz figures. Cernohorsky (1971: 186) gave a detailed synonymy, and *Cochlis onca* Röding, 1798, was shown to be the valid name. The Indo-Pacific *Naticarius onca* (Röding, 1798) was figured by Abbott & Dance (1982: 107, as *Natica*). Wood's name has sometimes been misdated as 1825.

glabra, Nerita – W. Wood, 1828b: 26, pl. 8, *Nerita* fig. 14; 45, as *Natica*. Loc.: Africa; Gray. Synonym of the Indo-Pacific *Tectonatica violacea* (G. B. Sowerby I, 1825), as recognized by Hanley (1856b: 232) and confirmed by Cernohorsky (1971: 189). Type material not located in NHMUK in 2010.

duplicata, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 1; 45, as *Natica*. The northwest Atlantic *Neverita duplicata* (Say, 1822).

intricata, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 7; 45, as *Natica*. This is *Natica intricata* Donovan, 1804.

patula, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 2; 45, as *Natica*. Name first made available as *Natica patula* G. B. Sowerby I, 1824 (*non N. patula* J. Sowerby, 1822). The Panamic *Hypterita helicoides* (Gray, 1825), a replacement name for G. B. Sowerby's taxon and type species of the genus (Keen, 1971: 47).

plumbea, Nerita – "W. Wood", 1828b: 25, pl. 8, *Nerita* fig. 3; 45, as *Natica*. The Australian *Natica plumbea* Lamarck, 1822, which is now regarded as a synonym of *Conuber sordidus* (Swainson, 1821) (Abbott & Dance, 1982: 102, as *Polinices*).

ASSIMINEIDAE

****francesii, Turbo*** – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 28; 47, as *Paludina*. Loc.: E. Indies; Gray. Reported from India in a revision of *Assiminea* as *A. francesii* Gray by Pease (1869: 166). Philippi (1844: 117) misspelled it as *Pauldina* "*francisci*." Concerning the origin of this name, see also Gray (1867), who is quoted in our remarks under the general discussion of Wood's *Supplement*. No later records of this species have been located. NHMUK 1907.9.25.5–15, 9 syntypes.

BARLEEIDAE

rufescens, Turbo – W. Wood, 1828b:19, pl. 6, *Turbo* fig. 13; 50, as *Pupa*. Loc.: Britain; Gray. Listed by Catlow & Reeve (1845: 142) without comment. Pfeiffer (1848b: 367) placed it in a list of unknown species. According to an added label with the type material, this may be a synonym of *Barleeia unifasciata* (Montagu, 1803). NHMUK 1984155, 2 syntypes.

POMATIOPSIDAE

unicarinatus, Turbo – "W. Wood", 1818: 144. This is *Cyclostoma unicarinata* Lamarck, 1816, based on same figure. This species is now placed in the genus *Tropidophora*.

STROMBIDAE

galea, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* figs. 13, 14. Loc.: unknown; NHMUK. Noted as a synonym of *S.* (*Tricornis*) *galeatus* Swainson, 1823, by Hanley (1856b: 215), a synonymy maintained for this Panamic species by Keen (1971: 421). The name probably originated as a misspelling. A syntype of *S. galea* Wood was isolated in NHMUK 1969332 by Wilkins (1957: 163), the smaller of the two specimens depicted by Wood.

incisus, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* fig. 12. Loc.: unknown; NHMUK. An Indo-Pacific species placed in the synonymy of *S.* (*Canarium*) *urceus*

Linnaeus, 1758, by Abbott (1960: 64–66). *Strombus* (*C.*) *urceus incisus* W. Wood (Kreipl & Poppe, 1999: 40). Type material not located in NHMUK in 2010.

jugosus, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 4. Loc.: Indian Ocean; NHMUK. Listed in the synonymy of *S.* (*Canarium*) *erythrinus rugosus* G. B. Sowerby I, 1825, by Abbott (1960: 81), an eastern subspecies of the Indo-Pacific *S. erythrinus* Dillwyn, 1817. Abbott listed Wood's species name as available, as did Hanley (1856b: 215), although it was probably just a misspelling of *rugosus* Sowerby. Type material not located in NHMUK in 2010.

****labiosus, Strombus*** – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 3. Loc.: unknown [restricted to Bataan, Luzon Id., Philippines (Abbott, 1960: 97)]; NHMUK. *Strombus* (*Dolomena*) *labiosus* W. Wood, 1828 (Abbott, 1960: 95–97; Kreipl & Poppe, 1999: 41). NHMUK 1953.3.12.1, holotype.

cancellatus, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 6; 51, as *Rostellaria*. This is *S. cancellatus* Lamarck, 1816, an Indo-Pacific species of *Varicospira* figured by Abbott & Dance (1982: 82).

dilatatus, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* fig. 20. Loc.: unknown; NHMUK. This is the Indo-Pacific *S. dilatatus* Swainson, 1821, as indicated by Hanley (1856b: 216).

floridus, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 5. This is *Strombus floridus* Lamarck, 1822.

gracilior, Strombus – W. Wood, 1828b: 13, pl. 4, *Strombus* fig. 1. As noted by Hanley (1856b: 214), this is the Panamic *S. gracilior* G. B. Sowerby I, 1825 (Keen, 1971: 420).

granulatus, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* fig. 21. As noted by Hanley (1856b: 216), this is the Panamic *S. granulatus* Swainson, 1823 (Keen, 1971: 421).

persicus, Strombus – W. Wood, 1828b: 14, pl. 4, *Strombus* fig. 19. This is *S. persicus* Swainson, 1821, as noted by Hanley (1856b: 216) and is not listed in synonymies as an available name of Wood (e.g., Abbott, 1960: 136).

unicornus, Strombus – "W. Wood", 1818: 115. This is a Dillwyn (1817) name, based on same figures in Chemnitz.

TONNIDAE

****tenue, Buccinum*** – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 4; 33, as *Cassis tenuis*. Loc: unknown; Mrs. Mawe. The Panamic *Cypraecassis tenuis* (W. Wood, 1828) (Keen, 1971: 500, as *Cassis*).

coarctatum, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 5; 1828b: 33, as *Cassis*. As noted by Hanley (1856b: 212), this is *Cassis coarctata* G. B. Sowerby I, 1825, a Panamic species (Keen, 1971: 501), now usually placed in the genus *Cypraecassis*.

recurvirostrum, Cassis – "W. Wood". An error by Reeve (1848) and Tryon (1885: 275) for *Buccinum recurvirostrum* Gmelin, 1791 [= *Phalium granulatum* (Born, 1778)].

ringens, Buccinum – "W. Wood", 1828b: 11, pl. 4, fig. 1; 38, as *Dolium*. Name first made available as *Dolium ringens* Swainson, 1822 (Wilkins, 1957: 162).

semigranosum, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 2; 33, as *Cassis*. Loc.: unknown; NHMUK. Name first made available by Lamarck as *Cassis semigranosa*. This Australian species, now known as *Phalium semigranosum* (Lamarck, 1822), was also wrongly attributed to Wood by Tryon (1885: 275), as noted by Wilkins (1958: 162).

tessellatum, Buccinum – "W. Wood", 1825 & 1828a: 105, pl. 22, fig. 27. This was intended to be *Cassis tessellatum* (Gmelin, 1791), as referenced by Wood (1818: 105). Abbott (1968: 128) listed Wood's name under the synonymy of *Phalium bisulcatum* (Schubert & Wagner, 1829) because Wood had figured a specimen of the latter in error.

HIPPONICIDAE

cassida, Patella – "W. Wood", 1818: 179. Name first made available by Dillwyn, 1817, who based it on same Favanne & Chemnitz figures cited by Wood. Synonym of the western Pacific *Hipponix conica* (Schumacher, 1817).

TRIVIIDAE

rosea, Cypraea – "W. Wood", 1828b: 9, pl. 3, *Cypraea* fig. 15. Name first made available by Gray, 1824.

VERMETIDAE [or Annelida]

rosea, Serpula – W. Wood, 1828b: 27; pl. 8, *Serpula* fig. 4. Loc.: unknown; Mrs. Mawe. The figure is indeterminate and could represent either a serpulid or vermetid. Only an examination of type material could resolve this.

conica, Serpula – "W. Wood", 1818: 186. This is *Serpula conica* Dillwyn, 1817, based on same figures cited by Wood. Present status of this name not determined.

fuscata, Serpula – "W. Wood", 1828b: 27; pl. 8, *Serpula* fig. 3. This is *Serpula fuscata* G. B. Sowerby I, 1825 (Hanley, 1856b: 234). This is a vermetid.

maxima, Serpula – "W. Wood", 1828b: 27, pl. 8, *Serpula* fig. 2; 58, as *Vermetus*. This is *Serpula maxima* G. B. Sowerby I, 1825 (Hanley, 1856b: 234), now placed in the vermetid genus *Dendropoma*.

RANELLIDAE

***labiosus, Murex** – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 18. Loc.: unknown; Mrs. Mawe. This wide-ranging [eastern South Africa to Hawaii; North Carolina to Brazil; Canary Islands, Cape Verde Islands] species was discussed by Beu (1998: 135–137) as *Cymatium* (*Turritriton*) *labiosum* (W. Wood, 1828). Beu stated that no "possible type material is now recognisable in NHMUK", but it would not be expected, as the original specimen was in the Mawe collection.

papilla, Murex – W. Wood, 1828b: 14, pl. 5, *Murex* fig. 2; 51 as *Ranella*. Loc.: unknown; NHMUK. Hanley (1856b: 216) indicated it to be a synonym of *R. verrucosa* G. B. Sowerby I, 1825, and this is correct (A. Beu, pers. comm., 13 Dec. 2009). NHMUK 20100624, holotype of both species (Dance, 1972: 160).

bitubercularis, Murex – "W. Wood", 1818: 121. Name first made available by Lamarck (1816; as *Ranella*) based on same figure in *Encyclopédie Méthodique*.

chlorostoma, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 20. As recognized by Hanley (1856b: 213), this is *Turbinella chlorostoma* G. B. Sowerby I, 1825, an Indo-Pacific species now placed in the genus *Peristernia*.

crassus, Murex – "W. Wood", 1818: 121. Name first made available by Dillwyn (1817) based on same figures in Chemnitz.

mulus, Murex – "W. Wood", 1818: 123. Name first made available by Dillwyn (1817); junior synonym of *Distorsio reticulata* Röding, 1798.

parthenopus, Murex – "W. Wood", 1818: 122. Made available by Dillwyn, 1817, who cited same Chemnitz figures as Wood. This is *Cymatium parthenopeum* (Salis Marschlins, 1793).

EPITONIIDAE

***martinii, Turbo** – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 20; 52, as *Scalaria*. Loc.: unknown; NHMUK. An Indo-Pacific species treated as *Filiscala martini* [sic] (W. Wood, 1828) by Wilson (1993: 279) and as *Amaea* (*Filiscala*) *martini* [sic] (W. Wood) by Weil et al. (1999). The broken holotype, NHMUK 20100591, was located in present study.

suturalis, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 41; 57, as *Turritella*. Loc.: unknown; NHMUK. Stated by Hanley (1856b: 225) to be a synonym of *Turritella spirata* G. B. Sowerby I, 1825. Although Wood's name has disappeared from the literature, the species is distinctive, with no doubt of the synonymy. Now classified in the Epitoniidae as *Eglisia spirata* (G. B. Sowerby, 1825), this is a West African species sometimes incorrectly listed as also occurring in the western Atlantic. Species figured by Weil et al. (1999: 36). Type material not located in NHMUK in 2010.

australis, Turbo – "W. Wood", 1828b: 19, pl. 6, *Turbo* fig. 18; 52, as *Scalaria*. This is *Scalaria australis* Lamarck, 1822.

fimbriatus, Turbo – "W. Wood", 1818: 149. This is *Scalaria fimbriata* Lamarck, 1816.

lamellosus, Turbo – "W. Wood", 1828b: 19, pl. 6, fig. 17; 52, as *Scalaria*. Name first made available as *Scalaria lamellosa* Lamarck, 1822.

principalis, Turbo – "W. Wood", 1818: 148. This is *Turbo principalis* Pallas, 1774.

raricostatus, Turbo – "W. Wood", 1828b: 19, pl. 6, *Turbo* fig. 16; 52, as *Scalaria*. A distinctive Indo-Pacific species, with Wood's name certainly a misspelling of *Scalaria raricosta* Lamarck, 1822. The addition of an extra syllable occurs in various places, most recently as *Variciscala raricostata* (Lamarck, 1822) by Wilson (1993: 1: 281).

varicosus, Turbo – "W. Wood", 1828b:19, pl. 6, *Turbo* fig. 19; 52, as *Scalaria*. This is *Scalaria varicosa* Lamarck, 1822, although Wood may have figured the wrong species. In any event, in *Turbo*, it is preoccupied by *Turbo varicosus* Brocchi, 1814.

BUCCINIDAE

curvirostris, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 26; 39, as *Fusus*. Loc.: unknown; NHMUK. Hanley (1856b: 218) stated this to be a synonym of *Murex corneus* Linnaeus, 1758, a Mediterranean species figured as *Buccinulum corneum* (Linnaeus, 1758) by Abbott & Dance (1982: 170). *Non Murex curvirostris* Wood, 1818 (see under Cerithiidae). Type material not located in NHMUK in 2010.

***distortum, Buccinum** – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 7; 50, as *Purpura*. Loc.: unknown; Mrs. Mawe. The Panamic *Triumphis distorta* (W. Wood, 1828) (Keen, 1971: 571).

***fragaria, Voluta** – W. Wood, 1828b: 11, pl. 3, *Voluta* fig. 27; 31, as *Buccinum*. Loc.: unknown; Mrs. Mawe. The Indian Ocean *Pollia fragaria* (W. Wood, 1828) (Abbott & Dance, 1982: 172).

***subrostratum, Buccinum** – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 9; 50, as *Purpura*. Loc.: unknown; Mrs. Mawe. The Panamic *Triumphis subrostrata* (W. Wood, 1828) (Keen, 1971: 572).

crassilabrum, Buccinum – "W. Wood", 1818: 115. This is *Monoceros crassilabrum* Lamarck, 1816, based on the same figure.

fulgurans, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 19; 55, as *Columbella*. As first recognized by Hanley (1856b: 218), this is *Columbella fulgurans* Lamarck, 1822, an Indian Ocean species placed in the synonymy of *Pyrene ocellata* (Link, 1807) by Abbott & Dance (1982: 161).

gemmulatum, Buccinum – "W. Wood", 1818: 115. This is *Purpura gemmulata* Lamarck, 1816.

melanostoma, Purpura – "W. Wood". An attribution error by Catlow & Reeve (1845: 272) for *Buccinum melanostoma* G. B. Sowerby I, 1825, which is now regarded as a *Cantharus*. It had been figured by Wood (1828b: pl. 4, fig. 3).

nodosum, Buccinum – "W. Wood", 1818: 103. This is *Buccinum nodosum* Dillwyn, 1817: 586.

norwegicum, Buccinum – "W. Wood", 1818: 115. Name first made available by Lamarck (1816), to whom Wood referred.

COLUMBELLIDAE

zebra, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 30; 34, as *Columbella*. Loc.: Pacific Ocean; Gray. *Non Buccinum zebra* Müller, 1774. Treated by Wilson (1994: 100) as a synonym of the Australian *Anachis miser* (G. B. Sowerby I, 1844). Type material not located in NHMUK in 2010.

terpsichore, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 21; 34, as *Columbella*. Name first made available as *Columbella terpsichore* G. B. Sowerby I, 1822, an *Anachis* from the Indian Ocean.

FASCIOLARIIDAE

acuminatus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 12; 57, as *Turbinella acuminata*. Loc.: unknown; Mrs. Mawe. *Non M. acuminatus* Pennant, 1777. Wood's species is a subjective synonym of the Panamic *Latirus mediamericanus* Hertlein & Strong, 1951 (Keen, 1971: 613). The latter is not a replacement name in the sense of ICZN *Code* Article 72.7 (Coan & Petit, 2006: 114).

***ceratus, Murex** – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 15; 57, as *Turbinella*. Loc.: unknown; Mrs. Mawe. This Panamic species is now treated as *Leucozonia cerata* (W. Wood, 1828) (Keen, 1971: 614).

rigidus, Murex – W. Wood, 1828b: 14, pl. 5, *Murex* fig. 3; 57, as *Turbinella*. Loc.: unknown; NHMUK. Considered a synonym of *Murex nodatus* Gmelin, 1791, by Hanley (1856b: 216) and subsequent authors. An Indo-Pacific species figured as *Latirus nodatus* (Gmelin, 1791) by Abbott & Dance (1982: 184). NHMUK 1974125, holotype.

***salmo, Murex** – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 14; 51, as *Pyrula*. Loc.: unknown; Mrs. Mawe. The Panamic *Fasciolaria salmo* (W. Wood) (Keen, 1971: 611).

***sanguineus, Murex** – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 10; 57, as *Turbinella*. Loc.: unknown; Mrs. Mawe. The Panamic *Latirus sanguineus* (W. Wood) (Keen, 1971: 614).

unifasciatus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 11; 57, as *Turbinella*. Loc.: unknown; Mrs. Mawe. Stated by Hanley (1856b: 218) to be a synonym of *Fasciolaria tarentina* Lamarck, 1822, which in turn is a synonym of *Fasciolaria lignaria* (Linnaeus, 1758). Wood's name has disappeared from the literature, except in a few lists of names. Linnaeus' Mediterranean species is figured by Poppe & Goto (1991: 158).

aplustre, Murex – "W. Wood, 1818" – Snyder (2003: 299) as = *Latirus amplustris* (Dillwyn, 1817). There is no "*aplustre* Wood, 1818", as that spelling appeared only in error in Wood 1828a (p. 129, *Murex* fig. 111) for the figure identified in 1818 and 1825 as *Murex amplustre*.

cariniferus, Murex – "W. Wood", 1818: 126. Name first made available by Lamarck (1816; as *Fusus*) based on same figure in *Encyclopédie Méthodique*.

granosa, Fasciolaria – "W. Wood" was attributed to Wood by Gray (1839: 114), but this name was proposed by Broderip, 1832.

longicaudus, Murex – "W. Wood", 1818: 125. Name first made available by Lamarck (1816; as *Fusus*) based on same figure in *Encyclopédie Méthodique*.

sinistralis, Murex – "W. Wood", 1818: 133. Name first made available as *Fusus sinistralis* Lamarck, 1816, based on the same figure in *Encyclopédie Méthodique*. Now regarded as a synonym of *Sinistralia maroccensis* (Gmelin, 1791).

NASSARIIDAE

***callosum, Buccinum** – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 14. Loc.: unknown; Mrs. Mawe. A South African species, figured by Abbott & Dance (1982: 177) as *Bullia callosa* (W. Wood, 1828) (also listed by Cernohorsky, 1984: 27).

noveboracensis, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 26; 31, as *B. noveboracense*. Loc.: America [presumably New York]; Gray. Synonym of *Ilyanassa obsoleta* (Say, 1822) (Cernohorsky, 1984: 40). NHMUK 20100606, 6 syntypes.

turris, Buccinum – W. Wood, 1818: 115. Based on Chemnitz (1786: pl. 124, figs. 1172–1173; pl. 125, figs. 1174–1175) and Lamarck (1816: pl. 394, fig. 6). Although all of these figures are of species of *Nassarius*, the first figure listed was included as a reference for species of *Cancellaria* by Gmelin and Lamarck (Petit, 1984: 59–60). Hanley (1856: 321) listed this species as of Wood "for *Nassa crenulata* [Lamarck], E.M. pl. 394, f. 6.", but he did not specifically restrict Wood's name to that figure. Because that Lamarckian figure best matches the shell later figured by Wood himself (1825: pl. 24, fig. 165), Wood's species is here restricted to Lamarck's figure under Article 24.2 (I.C.Z.N., 1999).

Under the heading "*Nassarius* (*Zeuxis*) *scalaris* (A.Adams, 1852) [nom. praeocc.]", Cernohorsky (1984: 136) listed *Buccinum turris* as of Wood, 1825, with Hanley's listing also included, and the statement "(*non* Wood 1818)". However, such separation is not possible because the references cited in all editions of Wood are identical except for the addition of a figure in 1825. The name as of Wood (1818) is not listed elsewhere in Cernohorsky's monograph. The first item in Cernohorsky's chresonymy is "1816. *Nassa crenulata* Lamarck … (*non Buccinum crenulatum* Bruguière, 1789 = *Nassarius*)." According to Cernohorsky, Bruguière's name is a *nomen dubium*, and itself is a junior primary honomym of *B. crenulatum* Linnaeus, 1758, a terebrid. Cernohorsky stated that Lamarck's use of the name *N. crenulata* is preoccupied by *Buccinum crenulatum* Bruguière, 1789, a *Nassarius*. In his discussion, he noted that: "All available taxa are homonyms and therefore not available, but no substitute name is proposed until more material for study will be available." However, *Buccinum turris* Wood, 1818, was, and remains, available but was not considered available by Cernohorsky as he had incorrectly made a distinction between Wood's 1818 and 1825 usages. The name *Nassarius scalaris* (A. Adams, 1852), belonging in the genus or subgenus *Zeuxis*, is still in use (Kool & Strack, 2000: 226), and the lectotype was figured by Cernohorsky (1984: pl. 26, fig. 6). The specimen figured by Lamarck, which is the type of *B. turris* Wood, should be in Musém d'Histoire Naturelle in Geneva. However, there are two individually numbered specimens there labeled as types of this species (MHNGINVE 77898), each representing a different species and neither corresponding to Lamarck's figure. It is possible that one of the names rejected for homonymy could be resurrected as one – *crenulata* – is a secondary homonym and the other – *scalaris* – is probably no longer considered congeneric. If homonymy stands as listed by Cernohorsky, *Buccinum turris* Wood, 1818, based on the figure in the *Encyclopédie Méthodique*, is not only available but is the valid name for the species now known as *Nassarius scalaris* (A. Adams, 1852) (confirmed by W. O. Cernohorsky, personal communication, August 2010).

abbreviata, Nassa – "W. Wood". Listed by Reeve (1854: expl. to pl. 29, fig. 194) attributed to Wood with Chemnitz as an additional reference, together with *Desmoulea* [sic] *abbreviata* Gray. First made available as *Buccinum abbreviata* Gmelin, 1791, a species now placed in *Demoulia* (Cernohorsky, 1984: 208).

lineolatum, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 22; 55, as *Terebra*. Name first made available as *Terebra lineolata* G. B. Sowerby I, 1825, now regarded as a synonym of *Bullia tanqubarica* (Röding, 1798) (Cernohorsky, 1984: 30).

verrucosum, Buccinum – “W. Wood”, 1818: 107, with reference to Lister, 1688: pl. 972, fig. 27; 1825 & 1828a: 107, pl. 22, fig. 45. Cernohorsky (1972: 135–136) unnecessarily listed this separately from *Buccinum verrucosum* Bruguière, 1789, which was based on the same figure in Lister. Cernohorsky (1972) declared *B. verrucosum* Bruguière to be a *nomen oblitum* in favor of *Nassarius graniferus* (Kiener, 1834), allowed under the ICZN *Code* at that time.

MELONGENIDAE

calcaratus, Murex – “W. Wood”, 1818: 124. Name first made available by Dillwyn (1817) based on same figures in Rumphius, etc.

colosseus, Murex – “W. Wood”, 1818: 125. This is *Fusus colosseus* Lamarck, 1816, type species of the genus *Hemifusus*.

MURICIDAE

aculeatus, Murex – W. Wood, 1828b: 15, 44, pl. 5, *Murex* fig. 19. Loc.: unknown; Mrs. Mawe. *Non M. aculeatus* Lamarck, 1822. Homonym renamed as *M. dubius* G. B. Sowerby I, 1841: 8, pl. [61], fig. 23, which is *non* Dillwyn, 1817. Due to homonymy, this eastern Pacific species was redescribed as *Muricopsis zeteki* by Hertlein & Strong (1951: 85–86) (see also Keen, 1971: 525). The latter is not a replacement name in the sense of ICZN *Code* Article 72.7 (Coan & Petit, 2006: 114).

armatum, Buccinum – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 12; 43, as *Monoceros*. Loc.: unknown; Mrs. Mawe. Synonym of the Panamic *Acanthina lugubris* (G. B. Sowerby I, 1822) (Keen, 1971: 552). Misspelled by Gray (1839: 124) as *B. amatum*.

****brevidentatum, Buccinum*** – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 10; 43, as *Monoceros*. Loc.: unknown; Mrs. Mawe. The Panamic *Acanthina brevidentata* (W. Wood, 1828) (Keen, 1971: 552).

cariosus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 22; 51, as *Purpura*. Loc.: unknown; Mrs. Mawe. *Non M. cariosus* Linnaeus, 1767. Synonym of the Indo-Pacific *Muricodrupa fenestrata* (Blainville, 1832) (Higo et al., 1999: 208).

cristatus, Murex – W. Wood, 1828b: 14, pl. 5, *Murex* fig. 4. Loc.: unknown; NHMUK. *Non M. cristatus* Brocchi, 1814. Synonym of *M. pinniger* Broderip, 1833 (Hanley, 1856b: 216). This Panamic species was figured as *Pterynotus pinniger* by Keen (1971: 526) and as *Purpurellus pinniger* (Broderip) by Radwin & D’Attilio (1976: 102) and by Abbott & Dance (1982: 141), none including this synonymy. Type material not located in NHMUK in 2010.

dentatum, Buccinum – W. Wood, 1818: 115. Based on the same figure in Lamarck (1816: pl. 396, fig. 5) named *Monoceros glabratum* Lamarck, 1816, and is therefore a junior synonym of it. Wood may have introduced a different name because he was using only Linnaean genera, and there was already a *Buccinum glabratum* Linnaeus. This is the Peru-Argentina species is now known as *Acanthina monodon* (Pallary, 1774).

denticulatum, Buccinum – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 11; 43, as *Monoceros*. Loc.: unknown; Mrs. Mawe. Synonym of the Panamic *Acanthina lugubris* (G. B. Sowerby I, 1822) (Keen, 1971: 552).

ferrugo, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 16. Loc.: unknown; Mrs. Mawe. A Red Sea and northern Indian Ocean species placed in synonymy of *Chicoreus virgineus* (Röding, 1798) by Houart (1992: 44).

funiculus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 17. Loc.: unknown; Mrs. Mawe. This is considered a synonym of the Indo-Pacific *Muricodrupa fiscella* (Gmelin, 1791) (Higo et al., 1999: 208).

subglobosus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 23. Loc.: unknown; Mrs. Mawe. Stated by Hanley (1856b: 218) to be a synonym of *Pyrula abbreviata* Lamarck, 1822, a species of *Coralliophila*. This western Atlantic shell was figured by Abbott & Dance (1982: 156).

****tectum, Buccinum*** – W. Wood, 1828b: 12, 51, pl. 4, *Buccinum* fig. 13; 51, as *Purpura*. Loc.: unknown; Mrs. Mawe. The Panamic *Cymia tecta* (W. Wood, 1828) (Keen, 1971: 552).

bulbosum, Buccinum – “W. Wood”, 1818: 111. This is *Buccinum bulbosum* Dillwyn, 1817, *ex* Solander ms; a junior synonym of *Rapana rapiformis* (Born, 1778).

costularis, Murex – “W. Wood”, 1828b: 14, pl. 5, *Murex* fig. 1. Stated by Hanley (1856b: 216) to be *Murex costularis* Lamarck, an Indo-West Pacific species listed as *Coralliophila costularis* (Lamarck, 1816) by Higo et al. (1999: 215).

foliatus, Murex – "W. Wood". Gray (1839: 109) listed this with reference to W. Wood (1828a: pl. 25, fig. 13) in a manner implying that Wood was the author of this Gmelin (1791) species. Gray was simply placing Wood's figure in the synonymy of *M. acanthopterus* Lamarck, 1816.

hippocastanum, Murex – "W. Wood", 1825 & 1828a: 124, pl. 26, fig. 53. Listed in the synonymy of *Drupa rubusidaeus* Röding, 1798, by Emerson & Cernohorsky (1973: 28). Wood intended to figure *Murex hippocastanum* Linnaeus, 1758, but figured the wrong species. This is thus a misidentification by Wood, not a new name.

hystrix, Murex – "W. Wood", 1825 & 1828a: 124, pl. 26, fig. 50. Listed in synonymy of *Drupa rubusidaeus* Röding, 1798, by Emerson & Cernohorsky (1973: 28). Wood intended to figure *Murex hystrix* Linnaeus, 1758, but figured the wrong species. Higo et al. (1999: 212), using this synonymy, spelled Wood's usage as *histrix*. This is merely a misidentification by Wood, not a new name.

imbricatum, Buccinum – "W. Wood", 1818: 115. This is *Monoceros imbricatum* Lamarck, 1816.

lacerus, Murex – "W. Wood", 1818: 124. Name first made available by Dillwyn (1817) based on same Chemnitz figure.

lingua, Murex – "W. Wood", 1818: 120. Name first made available by Dillwyn (1817) based on same Chemnitz figure.

morbosus, Murex – "W. Wood", 1818: 124. Name first made available by Dillwyn (1817) based on same figures in Chemnitz.

pinnatus, Murex – "W. Wood, 1828." Species attributed to Wood by Adam & Leloup (1938: 157) because they misdated Swainson's introduction of the name as 1832 instead of 1822.

plicatus, Murex – "W. Wood", 1818: 124. This is the same as *Murex plicatus* Dillwyn, 1817, based on same Chemnitz figures.

regius, Murex – "W. Wood", 1828b: 15. Name first made available by Swainson, 1821. Tryon (1880: 100) credited it to Wood, although Wood clearly referenced "Sw. Ex. Con. part 2."

rudolphi, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 6; 1828b: 50, as *Purpura*. Wood evidently intended to figure the Indo-Pacific *P. rudophi* Lamarck, 1822 [now *P. panama* (Röding, 1798)], but he figured the dissimilar Panamic *Purpura columellaris* Lamarck, 1816, instead. This was noted by Hanley (1856b: 212), who listed Wood's figure as of "Mawe (not Lam.)."

unifasciale, Buccinum – "W. Wood", 1818: 115. This is *Purpura unifascialis* Lamarck, 1816, based on same figure.

COSTELLARIIDAE

corrugata, Voluta – W. Wood, 1828b: 11, pl. 3, *Voluta* fig. 29; 43, as *Mitra*. Loc.: unknown; Mrs. Mawe. Synonym of the Indo-Pacific *Vexillum* (*Costellaria*) *exasperatum* (Gmelin, 1791) (Cernohorsky, 1970: 54–55).

ignea, Voluta – W. Wood, 1828b: 11, pl. 3, *Voluta* fig. 32; 43, as *Mitra*. Loc.: unknown; Mrs. Mawe. Synonym of *Vexillum* (*Costellaria*) *costatum* (Gmelin, 1791) (Cernohorsky, 1970: 54).

***unifasciata, Voluta** – W. Wood, 1828b: 11, pl. 3, fig. 28; 43, as *Mitra*. Loc.: unknown; Mrs. Mawe. The Indo-Pacific *Vexillum* (*Costellaria*) *unifasciatum* (W. Wood, 1828) (Cernohorsky, 1970: 55).

australis, Voluta – "W. Wood", 1828b: 10; pl. 3, *Voluta* fig. 15; 43, as *Mitra*. Name first made available by Swainson, 1820.

rigida, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 17; 43, as *Mitra*. Name first made available as *Mitra rigida* Swainson, 1821.

taeniata, Voluta – "W. Wood", 1818: 98. Name first made available as *Mitra taeniata* Lamarck, 1811.

vittata, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 10; 43, as *Mitra*. Name first made available as *Mitra vittata* Swainson, 1821 [not preoccupied by *M. vittata* Röding, 1798, a *nomen nudum*].

MARGINELLIDAE

castanea, Voluta – "W. Wood", 1818: 94. This is *Voluta castanea* Dillwyn, 1817, *non* Megerle von Muhlfeld, 1816. Dillwyn's species is presently regarded as a *nomen dubium* or a possible synonym of the West African *Marginella aurantia* Lamarck, 1822.

goodalli, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 7; 42, as *Marginella*. Name first made available as *Marginella goodalli* G. B. Sowerby I, 1825.

guttata, Voluta – "W. Wood", 1818: 93. Name first made available by Dillwyn, 1817.

marginata, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 8; 42, as *Marginella*. Name first made available by Born, 1778.

tessellata, Voluta – "W. Wood", 1828b: 11, pl. 3, *Voluta* fig. 31; 42, as *Marginella*. Name first made available as *Marginella tessellata* Lamarck, 1822.

HARPIDAE

harpa, Buccinum – "W. Wood, 1818: 107, pl. 22, f. 49." Listed in synonymy of *Harpa major* Röding, 1798, by Rehder (1973: 247), who also said: "Not *B. harpa* Linné, 1758." Oddly, Rehder referenced Wood (1818), but cited the plate and figure number from Wood 1825 & 1828a. This is just a misidentification by Wood, not a new name.

minus, Buccinum – "W. Wood", 1828b: 13, pl. 4, *Buccinum* fig. 24; 39, as *Harpa minor.* This was evidently intended to be *Harpa minor* Lamarck, 1822, misspelled on p. 13 as "*minus*". *Harpa minor* is now regarded as a synonym of the well-known Indo-Pacific *Harpa amouretta* Röding, 1798 (Rehder, 1973: 240–243). Attributed to Wood and incorrrectly placed in the synonymy of *Harpa crenata* Swainson, 1822, by Stearns (1894: 175).

roseum, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 23; 39, as *Harpa rosea.* This is *Harpa rosea* Lamarck, 1816, a West African species now placed in the synonymy of *Harpa doris* Röding, 1798 (Rehder, 1973: 255–256; Abbott & Dance 1982: 212). Attributed to Wood and incorrectly placed in synonymy of *Harpa crenata* Swainson, 1822, by Stearns (1894: 175).

MITRIDAE

filum, Voluta – W. Wood, 1828b: 11, pl. 3, *Voluta* fig. 30; 43, as *Mitra*. Loc.: unknown; Mrs. Mawe. Synonym of the Indo-Pacific *Mitra* (*Swainsonia*) *bicolor* Swainson, 1824 (Cernohorsky, 1991: 140–141).

lens, Voluta – W. Wood, 1828b: 11, pl. 3, fig. 25; 43, as *Mitra*. Loc.: unknown [designated as Santa Elena, Ecuador by Cernohorsky, 1976: 454]; Mrs. Mawe. Type not found (Cernohorsky, 1976: 454). The eastern Pacific *Mitra* (*Strigatella*) *lens* (W. Wood, 1828) (Keen, 1971: 640; Cernohorsky, 1976: 453–454).

pyramis, Voluta – W. Wood, 1828b: 10, pl. 3, *Voluta* fig. 16. Loc.: unknown; Mrs. Mawe. The Indo-Pacific *Mitra* (*Nebularia*) *pyramis* (W. Wood, 1828) (Cernohorsky, 1976: 424–425), who cited NHMUK 1967939, 2 possible syntypes of *Mitra cancellata* Swainson, 1821 (*non* Röding, 1798), as also being types of *V. pyramis*, but this is unlikely, as Wood figured material from the Mawe collection.

contracta, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 14; 43, as *Mitra*. Name first made available as *Mitra contracta* Swainson, 1820.

coronata, Voluta – "W. Wood", 1818: 99. Name first made available as *Mitra coronata* Lamarck, 1811 (Cernohorsky, 1976: 437–439). *Non Voluta coronata* Helbling, 1779.

costellaris, Voluta – "W.Wood", 1818: 97. Name first made available by Dillwyn, 1817.

crassa, Voluta – "W. Wood", 1828b: 10, pl. pl. 3, *Voluta* fig. 18; 43, as *Mitra*. Name first made available by Swainson, 1822 (Cernohorsky, 1976: 425–428).

fissurata, Voluta – "W. Wood", 1818: 96. Name first made available as *Mitra fissurara* Lamarck, 1811.

lugubris, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 12; 43, as *Mitra*. Name first made available as *Mitra lububris* Swainson, 1821 (Cernohorsky, 1976: 436–437).

radiatum, Buccinum – "W. Wood", 1825 & 1828a: 114, pl. 22, fig. 153. Name first made available as *Buccinum radiatum* Gmelin, 1791, based on the same figure in Gualtieri, a synonym of *Pterygia scabricula* (Linnaeus, 1758) (Cernohorsky, 1970: 42). Gmelin's introduction of *radiatum* in addition to Linnaeus' *scabriculum* is a result of Linnaeus, in 1758, having a *Murex scabriculum* and a *Buccinum scabriculum*. In 1767, he wished to placed both taxa in *Voluta* and introduced *Voluta cancellata* for the *Murex* (and in so doing introduced the misspelling *scabriusculus*), as discussed by Petit (1976: 34–35).

serpentina, Voluta – "W. Wood", 1825 & 1828a: 99, pl. 21, fig. 138. Synonym of the southwestern Pacific *Mitra puncticulata* Lamarck, 1811 (Cernohorsky, 1976: 447–448). *Non Mitra serpentina* Lamarck, 1811. Wood probably intended to illustrate *Mitra serpentina* Lamarck, but instead figured a specimen of *Mitra puncticulata* Lamarck, 1811.

zonata, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 13; 43, as *Mitra*. Name first made available as *Mitra zonata* Marryat, 1817 (Cernohorsky, 1976: 368).

OLIVIDAE

tenebrosa, Voluta – W. Wood, 1828b: 11, pl. 4, *Voluta* fig. 38. Loc.: S[outh] Sea; Mrs. Mawe. Synonym of the Panamic *Oliva* (*Strephonella*) *undatella* Lamarck, 1810 (Keen, 1971: 625; Tursch & Greifeneder, 2001: 467; Hunon et al., 2009: 232–233).

columellaris, Voluta – "W. Wood", 1828b: 11, pl. 4, *Voluta* fig. 34; 46, as *Oliva*. Name first made available as *Oliva columellaris* G. B. Sowerby I, 1825.

cruenta, Voluta – "W. Wood", 1818: 91. This is *Voluta cruenta* Dillwyn, 1817; a subjective synonym of *Oliva oliva* (Linnaeus, 1758).

erythrostoma, Voluta – "W. Wood", 1818: 91. Name first made available by Dillwyn, 1817.

incrassata, Voluta – "W. Wood", 1818: 92. Name first made available by Dillwyn, 1817.

marginatum, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 17; 30, as *Ancillaria*. This is *Ancillaria marginata* Lamarck, 1811, an Australian species treated as *Amalda marginata* (Lamarck, 1811) by Abbott & Dance (1982: 194).

micans, Voluta – "W. Wood", 1818: 92. This is *Voluta micans* Dillwyn, 1817.

oryza, Voluta – "W. Wood", 1818: 93. Name first made available as *Voluta oryza* Lamarck, 1822.

peruviana, Voluta – "W. Wood", 1828b: 11, Pl. 4, *Voluta* fig. 35. Name first made available as *Oliva peruviana* Lamarck, 1811.

tankervillii, Buccinum – "W. Wood", 1828b: 12, pl. 4, *Buccinum* fig. 16; p. 30, as *Ancillaria*. Name first made available as *Ancillaria tankervillii* Swainson, 1825. The western Atlantic *Amalda tankervillii* (Swainson, 1825).

tigrina, Voluta – "W. Wood", 1818: 92. Name first made available by Dillwyn, 1817.

ventricosa, Bulla – "W. Wood", 1818: 88. Name first made available as *Ancilla ventricosa* Lamarck, 1811.

OLIVELLIDAE

caerulea, Voluta – W. Wood, 1828b: 11, pl. 4, *Voluta* fig. 36; 46, as *Oliva*. Loc.: unknown; Mrs. Mawe. Hanley (1859b: 212) listed as a synonym of the Panamic *Olivella volutella* (Lamarck, 1811). This synonymy was confirmed by Burch & Burch (1960: 8).

****dama, Voluta*** – W. Wood, 1828b: 11, pl. 4, fig. 37; Loc.: "S. Sea"; Mrs. Mawe. The Panamic *Olivella dama* (W. Wood, 1828) (Keen, 1971: 628, as "*ex* Mawe ms").

nux, Voluta – W. Wood, 1828b: 11, pl. 4, *Voluta* fig. 33; 46, as *Oliva*. Loc.: unknown; NHMUK. Synonym of the Californian *Olivella biplicata* (G. B. Sowerby I, 1825) (Burch & Burch, 1960: 28). Type material not located in NHMUK in 2010.

PSEUDOLIVIDAE

bulbus, Buccinum – W. Wood, 1828b: 12, pl. 4, *Buccinum* fig. 8; 43, as *Purpura*. Loc.: unknown; Mrs. Mawe. Placed in synonymy of *Pyrula lineata* Lamarck, 1816, by Hanley (1856b: 212), a South African species now placed in *Melapium*.

TURBINELLIDAE

gravis, Voluta – "W. Wood", 1818: 101. Name first made available as *Voluta gravis* Lightfoot, 1786.

muricata, Voluta – "W. Wood", 1818: 100. Name first made available by Born, 1778.

VOLUTIDAE

flammula, Voluta – W. Wood, 1828b: 10, *Voluta* fig. 5. Based on a G. B. Sowerby I, 1825: pl. 3, fig. 1, of the Indonesian *Voluta cymbiola* Gmelin, 1791, and now considered to be a synonym of the same (Weaver & duPont, 1970: 76). Treated as *Cymbiola cymbiola* (Gmelin, 1791) by Abbott & Dance (1982: 216), with *V. flammula* in synonymy.

gracilis, Voluta – W. Wood, 1828b: 10, pl. 3, *Voluta* fig. 2; 59 (also on p. 43, as *Mitra*, in error; *pyramis* was the species intended to be listed there). Loc.: unknown; NHMUK. *Non Voluta gracilis* Swainson, 1821. Synonym of the Argentinean *Adelomelon ancilla* (Lightfoot, 1786) (Weaver & duPont, 1970: 102). NHMUK Sloane collection 2931, holotype.

modesta, Voluta – W. Wood, 1828b: 11, pl. 3, *Voluta* fig. 24. Loc.: unknown; Mrs. Mawe. Synonym of the Australian *Cymbiola flavicans* (Gmelin, 1791) (Weaver & duPont, 1970: 80–81; Wilson, 1994: 120).

angulata, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 21. Name first made available by Swainson, 1821.

harpa, Voluta – "W. Wood", 1828b: 11, pl. 3, *Voluta* fig. 26. Name first made available by Mawe, 1823.

imperialis, Voluta – "W. Wood", 1818: 100. Name first made available by Lightfoot, 1786.

junonia, Voluta – "W. Wood", 1818: 101. Name first made available by Lamarck, 1804.

lyriformis, Voluta – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 11; 43, as *Mitra*. Name first made available by Broderip, 1827.

punctata, *Voluta* – "W. Wood", 1828b: 10, pl. 3, *Voluta* fig. 19. Name first made available by Swainson, 1823.

CONIDAE

balteus, Conus – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 5. Loc.: unknown; Mrs. Mawe. A *nomen dubium* (Kohn, 1988: 47).

****brunneus, Conus*** – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 1. Loc.: unknown; Mrs. Mawe. The eastern Pacific *Conus* (*Conus*) *brunneus* W. Wood, 1828 (Keen, 1971: 661). Wood's figure designated as representative of the holotype by Kohn (1988: 48). Type locality: Galapagos Islands, designated by Coomans et al. (1982: 43).

gracilis, Conus – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 3. Loc.: Timor; Mrs. Mawe. *Non Conus gracilis* G. B. Sowerby I, 1823; renamed *Conus euschemon* by Tomlin (1937: 206). Wood's figure designated as representative of the holotype by Kohn (1988: 48), who treated it as a junior synonym of *Conus timorensis* Hwass in Bruguière, 1792.

****gradatus, Conus*** – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 6. Loc.: California; Mrs. Mawe. The Panamic *Conus* (*Leptoconus*) *gradatus* W. Wood, 1828 (Keen, 1971: 665). Wood's figure designated as representative of the lectotype and type locality restricted to Isla San Pedro Martir, Gulf of California, Mexico, by da Motta (1989). Kohn (1988: 48) considered it a *nomen dubium*.

interruptus, Conus – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 2. Loc.: unknown; Mrs. Mawe. Considered a synonym of *C. brunneus* W. Wood, 1828, by Kohn (1988: 49), who acted as first reviser in selecting the latter name as valid. Wood's figure 2 was designated representative of the holotype of *C. interruptus* by Kohn (1988: 48).

****lucidus, Conus*** – W. Wood, 1828b: 8, pl. 3, *Conus* fig. 4. Loc.: "South Sea"; Mrs. Mawe. The eastern Pacific *Conus* (*Cylindrus*) *lucidus* W. Wood, 1828 (Keen, 1971: 664–665). Wood's figure was designated representative of the holotype by Kohn (1988: 49).

acuminatus, Conus – "W. Wood", 1818: 69. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

aurantius, Conus – "W. Wood", 1818: 70. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, a work referenced by Wood.

catus, Conus – "W. Wood", 1818: 70 . Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

costatus, Conus – "W. Wood", 1818: 73. Name first made available by Dillwyn, 1817, based on same Chemnitz figure cited by Wood.

eburneus, Conus – "W. Wood", 1818: 67. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

fuscatus, Conus – "W. Wood", 1818: 67. Name first made available by Born, 1778; also treated by Dillwyn, 1817, based on figures referenced by Wood.

guinaicus, Conus – "W. Wood", 1818: 69. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

namocanus, Conus – "W. Wood", 1818: 73. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

pusillus, Conus – "W. Wood", 1825: 74, pl. 15, fig. 97. This is *C. pusillus* Lamarck, 1810. Listed by Hanley (1856: 82) and Carpenter (1864: 523) in a manner that implied that Wood had either figured the wrong species or created a homonym.

pyramidalis, Conus – "W. Wood", 1818: 77. Name first made available by Lamarck, 1810, based on figure in the *Encyclopédie Méthodique* referenced by Wood.

reticulatus, Conus – "W. Wood" – G. B. Sowerby I, 1834: 57, fig. 86 (*non* Born, 1778). This name was incorrectly attributed to Wood by Sowerby. An eastern Pacific species listed as *Conus reticulatus* Sowerby in the synonymy of *C. lucidus* Wood, 1828, by Keen (1971: 664).

roseus, Conus – "W. Wood", 1818: 74. Name first made available by Lamarck, 1810, based on figure in *Encyclopédie Méthodique* referenced by Wood.

taeniatus, Conus – "W. Wood", 1818: 71. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

tessellatus, Conus – "W. Wood", 1818: 67. Name first made available by Hwass in Bruguière, 1792, in the *Encyclopédie Méthodique*, which was referenced by Wood.

TEREBRIDAE

elongatum, Buccinum – W. Wood, 1828b: 13, pl. 4, *Buccinum* fig. 25; 55, as *Terebra*. Loc.: “India”; Mrs. Mawe. This mislocalized species was recognized as a synonym of the Panamic *Terebra strigata* G. B. Sowerby I, 1825, by Hanley (1856b: 214) and treated as such by Keen (1971: 684) and by Bratcher & Cernohorsky (1987: 127–128).

TURRIDAE

bicarinatus, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 7; 49 as *Pleurotoma*. Loc.: unknown; NHMUK. Renamed without reason as *Pleurotoma woodii* Kiener, 1840 (p. 12). Synonym of the Indo-Pacific *Turris cryptorrhaphe* (G. B. Sowerby I, 1825) (Powell, 1964: 336; Tucker, 2004: 125). NHMUK 1963470, holotype of both taxa (Dance, 1972: 160).

elegans, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 8; 49, as *Pleurotoma*. Loc.: unknown; NHMUK. *Non M. elegans* Donovan, 1804. Synonym of the Indo-Pacific *Lophiotoma polytropa* (Helbling, 1779) (Powell, 1964: 314). Powell provided measurements of Wood’s holotype, which is NHMUK 1970087.

***mitriformis, Murex** – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 25; 49, as *Pleurotoma curvirostris* in error (see below). Loc.: Isle of France [Mauritius]; Mrs. Mawe. Correct locality is West Africa. Now treated as *Genota mitriformis* (W. Wood, 1828) (Bernard, 1984: 205; Tucker, 2004: 673). Sometimes misspelled as “*mitraeformis*”.

pleurotoma, Murex – W. Wood, 1828b: 15, pl. 5, *Murex* fig. 9; 49, as *Pleurotoma*. Loc.: unknown; NHMUK. Hanley (1856b: 217) listed as “Wood, in place of *P. fusca*, Gray, MSS.—? *P. maura*, Reeve (as of Sow, Z.P.) C.S. [Conchologia Systematica] pl. 233, f. 4.” The name has disappeared from later literature, except for listings by Vokes (1971: 83) and Tucker (2004: 768) as “Turridae.” It is not *P. maura* as figured by Reeve and must be regarded as a *nomen dubium* unless Wood’s specimens come to light. Type material not located in NHMUK in 2010.

curvirostris, Pleurotoma – “W. Wood”, 1828b: 49, with reference to *Murex* pl. 5, fig. 25 – Evidently a transcription error for *Murex mitriformis*, the name for the species depicted in fig. 26 on that same plate (see above).

CLAVATULIDAE

mitra, Murex – W. Wood, 1828b: 14, pl. 5, *Murex* fig. 5; 49, as *Pleurotoma*. Loc.: unknown; NHMUK. Placed in synonymy of *Pleurotoma muricata* Lamarck, 1822, by Hanley (1856b: 217; Tucker, 2004: 635). This West African species figured as *Clavatula muricata* (Lamarck) by Abbott & Dance (1982: 242). Misspelled as *Murex mitratus* and *Pleurotoma mirata* by Deshayes (1843: 363). Type material not located in NHMUK in 2010.

DRILLIDAE

echinatus, Murex – “W. Wood”, 1828b: 14, pl. 5, *Murex* fig. 6; 49, as *Pleutoroma. Non M. echinatus* Brocchi, 1814. This is *Clavatula echinata* Lamarck, 1816, an Indo-Pacific species now considered a synonym of *Clavus flammulatus* Montfort, 1810 (Higo et al., 1999: 298).

CANCELLARIIDAE

buccinoides, Cancellaria – “W. Wood”, 1828 – Sneli & Stokland (1986: 123). An error for *Cancellaria buccinoides* G. B. Sowerby I, 1832.

BULLIDAE

elegans, Bulla – “W. Wood”, 1828b: 9. Name first made available as *Bulla elegans* Gray, 1825.

lineata, Bulla – “W. Wood”, 1828b: 9. Name first made available by Gray (1825).

priamus, Bulla – “W. Wood”, 1818: 88. This is *Bulla priamus* Dillwyn, 1817.

pyrum, Bulla – “W. Wood”, 1818: 87. This is *Bulla pyrum* Dillwyn, 1817.

PHILINIDAE

pectinata, Bulla – “W. Wood”, 1818: 86. Name first made available as *Bulla pectinata* Dillwyn, 1817: 481.

AMPHIBOLIDAE

australis, Turbo – W. Wood, 1828b: 18, pl. 6, *Turbo* fig. 7; 47, as *Paludina*. Loc.: New Holland; NHMUK. Placed in synonymy of *Ampullaria fragilis* Lamarck, 1822, by Hanley (1856b: 222). Listed, with a query, in synonymy of *Salinator fragilis* (Lamarck, 1822) by Hubendick (1945: 107) from southern Australia and Tasmania. Type material not located in NHMUK in 2010.

PLANORBIDAE

angulata, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 12; 49, as *Planorbis*. This is *Helix angulata* Rackett, 1821, a synonym of *Planorbis bicarinatus* Say, 1816 (Carpenter, 1886: 96), a homonym of *P. bicarinatus* (Lamarck, 1804). There is a litany of name changes for this species given in Abbott & Morris (1995: xxxi), in which the current name is stated to be *Helisoma anceps* (Menke, 1830), and it is also so listed in Turgeon et al. (1998: 135). It appears that recent workers have not noted that Rackett's name, long-buried in the synonymy of Say's species, predates that of Menke.

lacustris, Nautilus – "W. Wood", 1818: 63. Name first made available by Lightfoot (1786), a junior synonym of *Helix nitida* Müller, 1774.

SIPHONARIIDAE

angulata, Patella – "W. Wood", 1828b: 26, pl. 8, *Patella* fig. 1. First made available as *Siphonaria angulata* Gray, 1825, Wood probably obtaining the name from a label on a British Museum specimen. Synonym of the Panamic *Siphonaria gigas* G. B. Sowerby I, 1825 (Keen, 1971: 850).

SUCCINEIDAE

patula, Helix – "W. Wood", 1828b: 21; pl. 7, *Helix* fig. 9; 54, as *Succinea*. – This is *Bulimus patulus* Bruguière, 1789; now *Succinea patula* (Bruguière, 1789) from Guadeloupe.

PARTULIDAE

laevis, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 67; 32, as *Bulimus*. Loc.: Ceylon; NHMUK. Synonym of *Partula otaheitana* (Bruguière, 1792) from Tahiti (Pfeiffer, 1877: 204). Since its listing, with a query, in the synonymy of *Partula otaheitana* by Hartman (1885: 212), Wood's species has disappeared from the literature. Type material not located in NHMUK in 2010.

ACHATINELLIDAE

****byronii, Helix*** – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 30; 29, as *Achatina*. Loc.: Otaheite; Gray. This Hawaiian species is now placed in *Achatinella*. Figured by Abbott (1989: 59), but captioned in error as *Achatinella "bryonii"* (W. Wood, 1828), although he stated that it was named for Lord G. Byron, who collected it in 1824. NHMUK 20100497, 3 syntypes; NHMUK 20100498, 4 syntypes, both lots *ex* Gray collection.

PUPILLIDAE

edentulus, Turbo – "W. Wood", 1828b: 9, pl. 6, *Turbo* fig. 14; 50, as *Pupa*. This is *Pupa edentula* Draparnaud, 1805. Treated by Abbott (1989: 63) as *Columella edentula* (Draparnaud, 1805).

LAURIIDAE

anglicus, Turbo – "W. Wood", 1828b: 19, pl. 6, *Turbo* fig. 12; 50, as *Pupa*. Name first made available as *Vertigo anglica* Férussac, 1821, now *Leiostyla anglica* (Férussac, 1821). Name placed on the Official List of Specific Names in Zoology by Opinion 336 (1955) and attributed there incorrectly to Wood.

ENIDAE

labrosa, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 69; 32, as *Bulimus*. Name first made available as *Helix labrosa* Oliver, 1804, now placed in genue *Buliminus*.

pulchra, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 29; 32, as *Bulimus*. Name first made available as *Bulimus pulcher* Gray, 1825.

CLAUSILIIDAE

chrysalis, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 39; 34, as *Clausilia*. Loc.: West Indies; NHMUK. Sherborn (1925: 1255) followed the listing of Wood's name with "? Turt. 1810 [sic; = Turton, 1819]", but they are different species. Hanley (1856b: 224) attributed the name to Gray, with "*C. cretensis* Pfr. ii" as a synonym with a query and 'W. Indies' in single quotes. Hanley actually meant *C. cretensis* Rossmässler, as that is where Pfeiffer (1848b: 415) placed Wood's species. This taxon is now cited as *Albinaria cretensis* (Rossmässler, 1836), and it occurs in Crete and Greece (F. Welter-Schultes, personal communication, 12 May 2010). Type material not located in NHMUK in 2010.

costulatus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 36; 34, as *Clausilia*. Loc.: unknown; NHMUK. Placed in the synonymy of "*Nenia tridens* Chemnitz" by Pfeiffer (1881: 406–407). The earliest available name for this species is *Nenia tridens* (Schweigger, 1820). This Puerto Rican species was figured by Abbott (1989: 67).

mediterraneus, Turbo – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 40; 1828b: 34, as *Clausilia*. Loc.: Malta; NHMUK. Placed in synonymy of *Clausilia bidens* (Linnaeus, 1758) by Pfeiffer (1848: 453), together with *Helix papillaris* Müller, 1774, and the unavailable *T. papillaris* Chemnitz, a synonymy followed by Hanley (1856b: 224). In later years, Müller's name came into common usage, and an application for its conservation over Linnaeus' name was made to the I.C.Z.N. The application was turned down on a 13–14 vote, with the only two malacologists on the Commission voting in its favor. As a result, Opinion 2176 (I.C.Z.N., 2007) was issued placing *Turbo bidens* Linnaeus, 1758, on the Official List of Specific Names in Zoology, and this species is now known as *Papillifera bidens* (Linnaeus, 1758). NHMUK 20100488, syntypes, 7 specimens, *ex* Gray collection.

corrugatus, Turbo – "W. Wood", 1818: 152. This was a repeat of Dillwyn's listing, which was *Bulimus corrugatus* Bruguière, 1792, a clausilid now placed in *Albinaria.*

torticollis, Turbo – "W. Wood", 1828b: 20, pl. 6, *Turbo* fig. 35; 34, as *Clausilia*. This was *Bulimus torticollis* Olivier, 1801, placed in *Clausilia* by Lamarck, 1822.

truncatulus, Turbo – "W. Wood", 1828b: 20, pl. 6, *Turbo* fig. 37; 34, as *Clausilia*. Hanley (1856b: 224) listed this as a synonym of *Cylindrella collaris* (Féussac, 1821).This is *Clausilia truncatulus* Lamarck, 1822.

ORTHALICIDAE

****scobinata, Helix*** – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 77; 32, as *Bulimus*. Loc.: unknown; Mrs. Mawe. The Brazilian *Rhinus scobinata* (W. Wood, 1828) (Salgado & Coelho, 2003: 163; Simone, 2006: 129).

****vexillum, Helix*** – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 78; 32, as *Bulimus*. Loc.: unknown; Mrs. Mawe. Hanley (1856b: 230) gave the type locality as Peru, and this locality was confirmed by Pilsbry (1901: 159), who treated the species as *Drymaeus vexillum* (W. Wood). Sherborn (1932: 6889) listed *Helix vexillum* Férussac, 1821, but that was merely a change in genus of *Bulimus vexillum* Bruguière, 1792, and there is no homonymy.

guadeloupensis, Helix – "W. Wood" – Pfeiffer (1881: 246) credited this name to Wood in the synonymy of *Bulimulus exilis* (Gmelin, 1791). Why Wood's usage was selected and misspelled is not known, because Wood consistently (1818, 1825, 1828a: 167) used Bruguière's spelling. Gmelin's name is preoccupied and is a synonym of *Bulimulus guadaloupensis* (Bruguière, 1792), figured by Abbott (1989: 98, as *guadalupensis* [sic]).

odontostoma, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 25; 50, as *Pupa*. This is *Bulimus odontostoma* G. B. Sowerby I, 1824, now *Odontostomus odontostomus* (G. B. Sowerby I, 1824).

PLACOSTYLIDAE

kingii, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 27; 32, as *Bulimus*. Name first made available as *Bulimus kingii* Gray, 1825.

CERIONIDAE

albearia, Turbo – "W. Wood", 1818: 150; 1825: 150. Misspelling of *Turbo alvearia* Dillwyn, 1817, which is based on the same Lister figure; an unidentifiable *Cerion* according to Clench (1957: 137).

alveare, Turbo – "W. Wood", 1828a: 150, pl. 32, fig. 112. Placed with a query in synonymy of *Pupa maritima* Pfeiffer, 1839, by Pfeiffer (1849: 322). A misspelling, not a new name. See *Turbo albearia* "Wood."

UROCOPTIDAE

****formosus, Turbo*** – W. Wood, 1828b: 19, pl. 6, *Turbo* fig. 24; 31, as *Bulimus*. Loc.: W. Indies; Gray. Listed from Hispaniola in the genus *Macroceramus* by Wetherbee & Clench (1984:10). Type material not located in NHMUK in 2010.

****gracilis, Turbo*** – W. Wood, 1828b: 20, pl. 6, *Turbo* fig. 38; 34, as *Clausilia*. Loc.: West Indies; NHMUK. *Non Turbo gracilis* Brocchi, 1814. Wood's species was placed in *Cylindrella* by Pfeiffer (1848b: 381). This Jamaican species is now cited as *Apoma gracile* (W. Wood, 1828) (Rosenberg & Muratov, 2006: 156). The type of Brocchi's fossil species was figured by Rossi Ronchetti (1955: 154) as *Turbonilla* (*Pyrgolampas*) *gracilis*. To retain the name of the urocoptid, a petition to the I.C.Z.N. for conservation under Article 23.9.5 will be necessary because these homonyms have not been considered congeneric after 1899. Whatever action deemed necessary should be taken by specialists on the group. Type material not located in NHMUK in 2010.

*maugeri, Helix – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 31; 32, as *Bulimus*. Loc. W. Indes; Gray. Status in question. Listed by Rosenberg & Muratov (2006: 155) with a query under *Anoma nigrescens* (C. B. Adams, 1851), with a statement that it has priority if synonymy is correct. Type material not located in NHMUK in 2010.

cylindrus, Helix – “Wood” – Pfeiffer (1881: 276) credited this name to Wood in the synonymy of “*Cylindrella cylindrus* (*Turbo*) Chemnitz.” without a date or reference to Wood. Wood consistently (1818, 1825, 1828a: 150) treated this as *Turbo cylindrus* using references cited earlier by Dillwyn under this name, and the species is now known as *Urocoptis cylindrus* (Dillwyn, 1817). Figured by Abbott (1989: 122).

petiveriana, Helix – “W. Wood”, 1828b: 24, pl. 8, *Helix* fig. 70; 50, as *Pupa*. This is *Cylindrella petiveriana* (Pfeiffer, 1821)

ACHATINIDAE

bicarinata, Bulla – “W. Wood”, 1818: 89. Name first made available as *Bulimus bicarinata* Bruguière, 1792; placed in *Bulla* by Dillwyn (1817: 496).

columnaris, Lymnaea – “W. Wood”, 1828b: 41. Error for *Helix columna* Gmelin [= *Columna columna* (Müller, 1774)] when transferring to *Lymnaea*. Name was spelled correctly in 1828a.

undata, Helix – “W. Wood”, 1825 & 1828a: 167. Wood referred *Helix undata* Gmelin, 1791, which he attributed to “New Holland; Fr.w.” [= Australia; fresh water]. Not *H. undata* Lightfoot, 1786. *Nomen dubium*; possibly a young *Cochitoma*, according to Rehder (1967: 29).

FERUSSACIDAE

aurisvulpina, Voluta – “W. Wood”, 1818: 90. Name first made available by Holten, 1802 (Petit & Coan, 2008: 244).

SUBULINIDAE

calcarea, Helix – “W. Wood”, 1818: 165. This is *Helix calcaria* Born, 1778, the type species of *Neobeliscus* Pilsbry, 1896b.

STREPTAXIDAE

concamerata, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 21. Loc.: Cape of Good Hope; *ex* Férussac. Hanley (1856b: 227) listed this cryptically as “Wood for *H. pagoda* Fér.” Firmly placed in synonymy of *H. pagoda* Férussac, 1821, by Gray (1837: 486), where it has remained. Treated by Abbott (1989: 85) as *Gonidomus pagodus* (Férussac, 1821) with locality given as Mauritius.

ACAVIDAE

cornu, Helix – “W. Wood”, 1818: 155; 1825 & 1828a: 155, pl. 32, fig. 6. Loc.: New Zealand; ref. to Chemnitz (1795: pl. 208, figs. 2051, 2051). Listed here because the name was misattributed to Wood by Pfeiffer (1848a: 17) in the synonymy of the unavailable *Helix cornu giganteum* Chemnitz. The Chemnitz figures had earlier been named *H. cornu* by Dillwyn (1817: 888). Hanley (1856a: 163) listed *H. vesicalis* Lamarck as a synonym. This Madagascar species is in later literature as *Helix vesicalis* Lamarck, 1822, recently treated by Emberton (1990) as *Helicophanta vesicalis* (Lamarck, 1822), which is type species of that genus. We point out to those with an interest in the land mollusks of Madagascar that *Helix cornu* Dillwyn, 1817, is earlier than Lamarck's name for this species, which is based, in part, on the same Chemnitz figures.

CARYODIDAE

dufresnii, Helix – “W. Wood”, 1828b: 22, pl. 7, *Helix* fig. 28; 32, as *Bulimus*. This is *Bulimus dufresnii* Leach, 1815, now *Caryodes dufresnii* (Leach, 1815).

DORCASIIDAE

sinistrorsa, Helix – W. Wood, 1828b: 24, pl. 7, *Helix* fig. 60. Loc.: Cape of G. Hope. L.; “Fer. t. 32, f. 2, 3” [Férussac, 1820: pl. 32, figs. 2, 3]. This name was applied to a number of sinistral specimens by Férussac, all under the category “Monstrum”, and such names are not available (ICZN *Code* Art. 45.6). Wood's introduction was for a sinistral specimen of *H. globulus* Müller, 1774, according to Pfeiffer (1848a: 448) and Hanley (1859b: 229). This South African species is now *Trigonephrus globulus* (Müller, 1774). A normal dextral specimen was figured by Abbott (1989: 76).

STROPHOCHEILIDAE

goniostoma, Helix – "W. Wood", 1828b: 22, pl. 7, *Helix* fig. 24. This is *H. goniostoma* Féussac, 1821, now placed in genus *Gonystomus*.

HELICARIONIDAE

meridionalis, Helix – W. Wood, 1828b: 23, pl. 7, *Helix* fig. 42. Loc.: Otaeti [= Tahiti]; "Fer. t. 29, f. 4, 5, (*otahietana*)" [Férussac, 1820: pl. 29, figs. 4, 5; 1821: pl. expl.]. Wood probably renamed this Férussac species because *Bulimus otaheitanus* Bruguière, 1792, had been transferred to *Helix* by Dillwyn (1817: 935). This Philippine species was treated as *Ryssota otaheitana* [sic] (Férussac, 1821) by Abbott (1989: 129). Spellings of specific name are as published.

ARIOPHANTIDAE

laevipes, Helix – "W. Wood", 1818: 155. In Sherborn (1927: 3369), as "*Turbo*". Name first made available as *Helix laevipes* Müller, 1791, the type species of *Ariophanta* Des Moulins, 1829.

BULIMULIDAE

****dentata, Helix*** – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 71; 50, as *Pupa*. Loc.: unknown; NHMUK. This species occurs in Argentina and Uruguay and is type species of the genus *Plagiodontes* Doering, 1875 (subsequent designation of Pilsbry, 1898) (Pizá & Cazzaniga, 2010, in press). NHMUK 1840.9.12.50, 2 syntypes, 1 broken.

listeri, Helix – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 23; 32, as *Bulimus*. Loc.: unknown; NHMUK. Synonym of the Brazilian *Auris melastoma* (Swainson, 1820) (Pilsbry, 1896a: 103; Simone, 2006: 132). Type material not located in NHMUK in 2010.

CAMAENIDAE

orbiculata, Helix – W. Wood, 1828b: 20, pl. 7, *Helix* fig. 2. Loc.: West Indies; ref. to "Fér. t. 42, f. 4. (*plicaria*)" [Férussac, 1822: pl. 42, fig. 4; 1821, pl. expl.]. Wood probably renamed this Férussac figure, labeled as *H. plicaria* Lamarck, due to a prior *Helix plicaria* Born, 1780. However, that Born usage is not available as it was a misspelling by Born of his own 1778 *H. plicata*. Moreover, there was already an unrelated *Helix orbiculata* Férussac, 1821. Abbott (1989: 191, 140, respectively) figured both the camaenid *Hemicycla plicaria* (Lamarck, 1816) and the helicid *Pleurodonte orbiculata* (Férussac, 1821). Wood's own figure does not agree well with either, but his name should probably be considered a synonym of Lamarck's species, given his reference to Férussac's figure of it.

zonula, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 8. Loc.: Ceylon; ref. to "Fer. t. 26, f. 6 (*vittata* n. 35)" [Férussac, 1820: pl. 26, fig. 6; 1821, pl. expl.]. Wood renamed *H. vittata* Férussac, 1821, due to prior usage of the name by Müller (1774). However, as was noted very early, the names of Férussac and Müller are synonyms as well as homonyms. Wood's synonym has disappeared from the literature, but it was included in a long synonymy of *Planispira vittata* (Müller, 1774) by Gude (1914: 164) that includes Férussac's *H. vittata* and Wood's *H. zonula*.

formosa^1*, Helix* – "W. Wood", 1828b: 20, 39, pl. 7, *Helix* fig. 1. This is one of two appearances of this name combination in Wood, this one indicated by Wood with a superscript "1" (for the other, see under Helicidae). Name first made available as *Helix formosa* Férussac, 1821, the figure for which was cited by Wood. The West Indian *Pleuodonte formosa* (Férussac, 1821).

listerae, Carocolla – "W. Wood", 1828b: 33. An error by Wood for *Carocolla listeri* Gray, 1825. See also next entry.

listeriana, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 61. Also an error by Wood for *Carocolla listeri* Gray, 1825.

plicata, Helix – "W. Wood", 1818: 156. This is *Helix plicata* Dillwyn, 1817, a subjective synonym of *Labyrinthus otis* (Lightfoot, 1786).

soror, Helix – "W. Wood", 1828b: 23, pl. 7, *Helix* fig. 51; 33, as *Carocolla*. Name first made available as *Helix soror* Férrusac, 1821.

VITRINIDAE

fuscescens, Helix – "Wood" – Pfeiffer (1881: 28) listed this name in synonymy of *Helicolimax pellicula* Férussac, 1821, with a query. No date or reference to Wood is given, but Wood treated *Helix fuscescens* Gmelin, 1791, in 1818: 165, 1825 & 1828a: 165, pl. 34, fig. 133. In each citation, Wood referred to Gmelin, and the name is thus not attributable to Wood.

HELICIDAE

carina, Helix – W. Wood, 1828b: 23, pl. 7, *Helix* fig. 57. Loc.: E. Indies; ref. to "Fer. t. 60, f. 2. (*Lampas*)" [Férussac, 1822: pl. 60, fig. 2; pl. expl.]. It is not known why Wood renamed this species, because Férussac cited Müller and Dillwyn, as well as a figure in Chemnitz. Possibly he considered that Férussac's figure was not the same as that of Chemnitz. Certainly all later authors have considered *H. carina* to be a synonym of *H. lampas* Müller, 1774, a species of *Carocolla*.

exalbida, Helix – W. Wood, 1828b: 25, pl. 8, *Helix* fig. 81. Loc.: unknown; Mrs. Mawe. Recognized by Hanley (1856b: 230) as a synonym of *H. nivosa* G. B. Sowerby I, 1824, a Madeiran species now placed in the genus *Leptaxis*.

fibula, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 66. Loc.: Sicily; NHMUK. Placed in the synonymy of *Helix conoidea* Draparnaud, 1801, by Tryon (1888: 31–32), a species now placed in the genus *Cochlicella*. Type material not located in NHMUK in 2010.

formosa*[2]*, Helix – W. Wood, 1828b: 21, 40, pl. 7, *Helix* fig. 10; Loc.: unknown; ref. to "Fer. t. 31, f. 4, 5, 6" [Férussac, 1820: pl. 31, figs. 4–6; 1821: pl. expl.]. This was one of two appearances of this same name combination in Wood, this one indicated by Wood with a superscript "2" (for the other, see under Camaenidae). *Non Helix formosa* Férussac, 1821. Synonym of *Helicostyla mirabilis* (Férussac, 1821), based on the figures cited by Wood. This Philippine type species of *Helicostyla* was figured by Abbott (1989: 173).

helicella, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 7. Loc.: Morocco; ref. to "Fer. t. 30, f. 2 (*planata* 295)" [Férussac, 1820: pl. 30, fig. 2; 1821: pl. expl.]. Wood renamed *H. planata* Férussac, 1821, due to prior usage of the name by Maton & Rackett (1807). His name is still in use as *Theba subdentata helicella* (W. Wood, 1828) and was treated and figured by Gittenberger & Ripken (1987: 23).

madeirensis, Helix – W. Wood, 1828b: 25, pl. 8, *Helix* fig. 84. Loc.: Madeira; Mrs. Mawe. A common Madeiran species listed as *Disculella maderensis* [sic] (W. Wood, 1828) by Walden (1983: 267). Lowe (1831: 48, 69) also misspelled this name as *Helix* "*maderensis*" when he included it in his genus *Ochthephila*, as did Beck (1837: 18).

scabra, Helix – W. Wood, 1828b: 24, pl. 8, *Helix* fig. 62. Loc.: W. Indies; NHMUK. *Non H. scabra* Linnaeus, 1758. Hanley (1856b: 229) noted that this was *Helix undata* Lowe, 1831, and also *Helix groviana* Férussac, 1821. Lowe (1831: 41) introduced the new name *H. undata*, with *H. scabra* Wood in synonymy, but did not state that he was proposing a replacement name. This is a Madeiran species, placed in *Leptaxis* by Cockerell (1921: 194), who pointed out that *H. undata* is also preoccupied and the species must be known as *Leptaxis groviana* (Férussac, 1821). Why Férussac's name, obviously earliest, had not been in use before is not known. Type material not located in NHMUK in 2010.

tripolitana, Helix – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 33. Loc.: Tripoli; Gray. Listed as a "keeled form" of *Levantina leachi* (Férussac, 1821) by Goodfriend (1986: 215). Type material not located in NHMUK in 2010.

turgidula, Helix – W. Wood, 1828b: 21, pl. 7, *Helix* fig. 6. Loc.: Europe; "Fer. t. 29, f. 12" [sic] [Férussac, 1820: pl. 29, figs. 1, 2; 1821: pl. expl.]. Recognized by Hanley (1856b: 225) as a "monstrous *arbustorum*" this is a high-spired freak of *Arianta arbustorum* (Linnaeus, 1758). Listed by Férussac as one of two "Monstrum" varieties of *H. arbustorum* Linnaeus, but unavailable as it was intended as a name for a teratological specimen (ICZN *Code* Article 1.3.2). As Wood made no such statement, the name is available from him, although invalid as a junior synonym, simply being a high-spired freak of *Arianta arbustorum* (Linnaeus, 1758). Normal specimens were figured by Abbot (1989: 190).

ligatus, Turbo – "W. Wood", 1818: 151. This is *Turbo ligatus* Dillwyn, 1817, based on same Chemnitz figure.

portosanctana, Helix – "W. Wood", 1828b: 24, pl. 8, *Helix* fig. 79 [originally as *porto sanctana*]. This is *Helix portosanctanae* G. B. Sowerby I, 1824.

punctulata Helix – "W. Wood", 1828b: 25, pl. 8, *Helix* fig. 80. Name first made available by *Helix punctulata* G. B. Sowerby I, 1824.

tectiformis, Helix – "W. Wood", 1828b: 25, pl. 8. Name first made available as *H. tectiformis* G. B. Sowerby I, 1824.

BRADYBAENIDAE

ventricosus, Orthostylus – "W. Wood". Listed by Sherborn (1932: 6846) as a transfer of "*Bulla ventricosa* Wood" to *Orthostylus* by Beck (1837: 49). This was an error by Sherborn, because Beck's listing was of *Bulimus* *ventricosus* Bruguière, 1792, with no mention of Wood; this is a tree snail now known as *Helicostyla ventricosa* (Bruguière, 1792). Wood did list a *Bulla ventricosa* (Lamarck, 1811), a member of the Olividae, also misattributed to Wood by Sherborn.

HYGROMIIDAE

***bulverii, Helix** – W. Wood, 1828b: 25, pl. 8, *Helix* fig. 82. Loc.: unknown; Mrs. Mawe. Now classified as *Discula bulverii* (W. Wood, 1828), this species from Madeira, Portugal, is on the IUCN Red List of Threatened Species. Lowe (1831: 44, 68) made an unjustified emendation of this name to *Helix bulveriana*, and Beck (1837: 28) misspelled it as *Chilotrema* "*bulweri*".

PLEURODONTIDAE

granosa, Helix – W. Wood, 1828b: 23, pl. 7, *Helix* fig. 45. Loc.: America; "Fer. t. 44, f. 1–3, (*aspera*)" [Férussac, 1821: pl. 44, figs. 1–3; pl. expl.]. Wood renamed Férussac's species, probably due to the prior *Helix aspera* Gmelin, 1791. Placed in the synonymy of *Helix aspera* Férussac by Pfeiffer (1848a: 311). This is a Jamaican species treated as *Thelidomus aspera* (Férussac, 1821) by Rosenberg & Muratov (2007: 401). A petition to the I.C.Z.N. would be needed to conserve *Helix aspera* Férussac, 1821, an action left for specialists familiar with the taxa involved.

***nigrescens, Helix** – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 32; Loc.: unknown; Wood collection. Treated as *Pleurodonte nigrescens* (W. Wood, 1828) by Robinson et al. (2006: 643), who gave locality as Guadeloupe and Dominica.

HELMINTHOGLYPTIDAE

squamosa, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 3. Loc.: W. Indies; ref. to "Fer. t. 41. f. 3" [Férussac, 1821: pl. 41, fig. 3; pl. expl]. Name first made available as *Helix squamosa* Férussac, 1821, the figure for which was cited by Wood. The Antillean type species of *Bellacepolis* Pilsbry in Baker, 1943.

POLYGYRIDAE

sayii, Helix – W. Wood, 1828b: 22, pl. 7, *Helix* fig. 34. Loc.: N. America; Gray. Thought by Hanley (1856b: 228) to be a synonym of *Polygyra avara* Say, 1818, this eastern North American species was considered by Pilsbry (1940: 601, 603) to be a possible senior synonym of *Daedalochila postelliana* (Bland, 1859). Type material not located in NHMUK in 2010.

fraterna, Helix – "W. Wood", 1828b: 21 & 40, pl. 7, *Helix* fig. 16. Loc.: land, N. America; Wood collection. The figured specimen was evidently intended to represent *Helix fraterna* Say, 1824. However, according to Green (1830: 135) and Hanley (1856b: 226), it was instead a misidentified specimen of the eastern United States *Helix hirsuta* Say, 1817. The former is now *Euchemotrema fraternum* (Say, 1824), the latter *Stenotrema hirsutum* (Say, 1817) (Turgeon et al., 1998: 151, 153).

monodon, Helix – "W. Wood", 1828b: 21; pl. 7, *Helix* fig. 15. Name first made available as *Helix monodon* Rackett, 1821.

septemvolva, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 14. Name first made available and still known as *Polygyra septemvolva* Say, 1818 (Turgeon et al., 1998: 152).

tridentata, Helix – "W. Wood", 1828b: 21, pl. 7, *Helix* fig. 11. Name first made available as *Helix tridentata* Say, 1818, which is now placed in *Triodopsis*.

POLYPLACOPHORA

bistriatus, Chiton – W. Wood, 1814: 7. Loc.: unknown [designated as Gambier, Providence Id., Bahama Ids. (Bullock, 1988a: 153)]. Cited figures in Chemnitz (1784: pl. 1, fig. 1; 1785: pl. 94, figs. 788–791). Type not known (Bullock, 1988a: 153). Synonym of western Atlantic *Chiton tuberculatus* Linnaeus, 1758 (Kaas & Van Belle, 1980: 17; Bullock, 1988a: 152–155; Kaas et al., 2006: 73–75).

capensis, Chiton – W. Wood, 1828b: 1, pl. 1, *Chiton* fig. 11. Loc.: C[ape] of Good Hope; NHMUK. Not *C. capensis* Schröter, 1801. Placed in synonymy of *Radsia nigrovirescens* (Blainville, 1825) by Bullock (1988b: 287), who stated that the type of Wood's species was not found in the British Museum but that the types of *C. capensis* Gray, 1828, are present, numbered NHMUK 1951.2.1.9, 4 syntypes. These, however, are Wood's types. See also Kaas et al. (2006: 84–86).

carmichaelis, Chiton – W. Wood, 1828b: 1, pl. 1, *Chiton* fig. 10. Loc.: "C[ape] of Good Hope"; NHMUK. Type locality corrected to Tierra del Fuego by Gray (1847a). Misattributed to Gray

(1828), whose description was published after that of Wood (1828b), this species was treated by Ferreira (1982) and by Kaas & Van Belle (1994: 266–269). A lectotype (NHMUK 1951.1.25.1) was designated by Ferreira (1982), the specimen probably that figured by Wood; NHMUK 1951.1.25.2, paralectotype. Species figured by Forcelli (2000: 182), who also misattributed it to Gray. Type species of *Plaxiphora* Gray, 1847. The oldest name for this species is *Plaxiphora aurata* (Spalowsky, 1795) (Kaas & Van Belle, 1994), and it occurs in New Zealand and adjacent islands, the Falkland Islands, and in the Magellanic province of South America.

castaneus, Chiton – W. Wood, 1814: 13–14, pl. 2, figs. 2, 3; pl. 3, fig. 2, 3. Loc.: unknown; at least pl. 2 figs. from collection of [H. C.] Jennings. Synonym of the South African *Callochiton dentatus* (Spengler, 1797); *C. castaneus* used in many earlier references (Kaas & Van Belle, 1985: 15–17).

fasciatus, Chiton – W. Wood, 1814: 10; pl. 1, figs. 4, 5. Loc: "South America" [corrected to be Robins Bay, St. Mary, Jamaica (Bullock, 1988a: 178)]; figured specimen from [H. C.] Jennings collection; type presumed lost (Bullock, 1988a: 178). Wood also cited Chemnitz (1784: pl. 1, fig. 3; 1785: pl. 94, fig. 792, pl. 96, fig. 801). Synonym of the western Atlantic *Chiton* (*Diochiton*) *squamosus* Linnaeus, 1764 (Kaas & Van Belle, 1980: 46; Bullock, 1988a: 178–179; Kaas et al., 2006: 76–78).

fulvus, Chiton – W. Wood, 1814: 7–8. Loc.: unknown. Cited Chemnitz (1788: pl. 173, fig. 1691) and Bruguière (1792: pl. 161, figs. 4, 5). Synonym of the eastern South American *Chaetopleura angulata* (Spengler, 1797) (Kaas & Van Belle, 1988: 282; Rios, 1994: 16).

***lineatus, Chiton** – W. Wood, 1814: 15–16, pl. 2, figs. 4, 5. Loc.: unknown [restricted to Sitka, Alaska (Sirenko, 1974: 994); further restricted to Starrigaven Bay, Sitka (Clark, 1999: 34)]; figured specimen from [H. C.] Jennings collection; type lost (Ferreira, 1982); neotype: LACM 2734 (Clark, 1999: 34). The northeastern Pacific *Tonicella lineata* (W. Wood, 1815) (Clark, 1999: 34–36; Eernisse et al., 2007: 711).

luteolus, Chiton – W. Wood, 1828b: 1, *Chiton* fig. 3. "Indian Ocean" [St. Croix, Virgin Islands – Bullock, 1988b: 172]; Mrs. Mawe. *Nomen dubium* (Kaas & Van Belle, 1980: 78), but later listed as a synonym of *Chiton* (*Chiton*) *viridis* Spengler, 1797 (Bullock, 1988b: 172; Kaas et al., 2006: 81–84).

***nebulosus, Chiton** – W. Wood, 1828b: 1, pl. 1, *Chiton* fig. 4. Loc.: Isle of France [Mauritius]; Mrs. Mawe. Possible synonym of *Acanthopleura borbonica* (Deshayes, 1863) (Kaas & Van Belle, 1980: 89; Kaas et al., 2006: 266–268); possible senior synonym of *Chiton mauritianus* Quoy & Gaimard, 1835 (D. Eernisse, personal communication, 6 Nov. 2009).

setosus, Chiton – W. Wood, 1828b: 1, pl. 1, *Chiton* fig. 5. Loc.: W. Indies; Mrs. Mawe. *Non Chiton setosus* Tilesius, 1824 (and *non C. setosus* G. B. Sowerby I, 1832). Synonym of *Ceratozona squalida* (C. B. Adams, 1845), which occurs in both the western Atlantic and eastern Pacific (Ferreira, 1985: 200–202).

siculus, Chiton – W. Wood, 1828b: 1, pl. 1, *Chiton* fig. 12. Loc.: coast of Sicily; NHMUK. Synonym of the European *Chiton* (*Rhyssoplax*) *olivaceus* (Spengler, 1797) (Kaas & Van Bell, 1980: 119; Kaas et al., 2006: 151–154). Two lots of probable syntypes, 2 specimens (NHMUK 20100597) and 3 specimens (NHMUK 20100598) on cards found during present study.

***sulcatus, Chiton** – W. Wood, 1814: 16–17, pl. 3, fig. 1. Loc.: "South Seas" [restricted to Isla San Xalvador, Islas Galápagos (Bullock, 1988a: 160)]; Mrs. Robinson's collection; type presumed lost (Bullock, 1988: 160). *Non Chiton sulcatus* Quoy & Gaimard, 1835; unnecessarily renamed *Chiton woodii* Clessin, 1903, because of this later homonym. *Chiton sulcatus* W. Wood, 1815, occurs in the Islas Galápagos (Keen, 1971: 864; A. G. Smith & Ferreira, 1977: 89–90; Kaas & Van Belle, 1980: 128; Bullock, 1988a: 160–161; Kaas et al., 2006: 145–147). It should be noted that p. 16 and pl. 3 appeared in 1814; it cannot be proven that p. 17 appeared that year, although it probably did.

tessellatus, Chiton – W. Wood, 1815: 23, *ex* Leach ms. Loc.: not stated [designated as Gambier, Providence Id., Bahama Ids. (Bullock, 1988a: 153)]; type not known (Bullock, 1988: 153). Wood cited Chemnitz (1788: pl. 173, fig. 1690) and Bruguière (1792: pl. 162, fig. 10). Synonym of western Atlantic *Chiton tuberculatus* Linnaeus, 1758 (Kaas & Van Belle, 1980: 131; Bullock, 1988a: 152–155; Kaas et al., 2006: 73–75).

***tunicatus, Chiton** – W. Wood, 1814: 11–12, pl. 2, fig. 1. Loc.: unknown. The northeastern Pacific *Katharina tunicata* (W. Wood, 1815) (Kaas & Van Belle, 1994: 349–351; Eernisse et al., 2007: 711); type species of *Katharina* Gray, 1847. NHMUK 1837.12.1.3136, holotype (Gray, 1847a: 69).

CEPHALOPODA

bullata, Argonauta – "W. Wood", 1818: 62. This one is unfathomable. Wood's only reference is to Gualtieri (1742: pl. 79, fig. C), a plate composed of figures of *Pinna*, so this must have been an error. Dillwyn (1817: 333–337) treated nine species of *Argonauta*, giving names for all of the species on Gualtieri's Plate 12, and this list of nine was copied by Wood (1818: 62). Wood's 10th species is *bullata*, and the 11th and last, is a repeat of the 8th. *Argonauta bullata* was also included in Wood (1823: 62), but it was omitted in Wood (1828a: 62), which includes only Dillwyn's nine species. *Argonauta bullata* Wood, 1818, 1823, seems not to be mentioned in subsequent literatue. In the absence of a figure or description, it must be considered a *nomen nudum*.

haustrum, Argonauta – "W. Wood", 1818: 62. Based on Chemnitz figure included in *Argonauta haustrum* Dillwyn, 1817, which is now regarded as a probable synonym of *Argonauta hians* Lightfoot, 1786.

ACKNOWLEDGMENTS

We appreciated the help of many persons who provided assistance and advice on aspects of this project. These include Kathie Way, Amelia McClellan, Suzanne Williams, and Jonathan Ablett of The Natural History Museum, London; Jackie Woodruff of St. Martins, Ruislip; as well as Benjamin Bather, Rüdiger Bieler, Paul Callomon, Walter O. Cernohorsky, Robert Cowie, Douglas Eernisse, Yves Finet, Lindsay Groves, Markus Huber, Alan R. Kabat, Pierre Lozouet, Konstantin Lutaenko, Jan Johan ter Poorten, Gary Rosenberg, John Tucker, Francisco Welter-Schultes, and two anonymous reviewers.

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	4	137–196	16–20	Aug. 1883
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	7	259–298	31–35	Aug. 1884
	8	299–342	36–40	Sept. 1884
	9	343–386	41–45	Feb. 1885
	10	387–418	46–50	Aug. 1885
	11	419–454	51–55	Jan. 1886
	12	455–486	56–60	April 1886
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2	14	1–24	1–6	Nov. 1887
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	16	61–112	12–21	May 1889
	17	113–172	22–29	April 1890
	18	173–220	30–37	April 1891
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WOOD, W., 1835, *General conchology; or, a description of shells, arranged according to the Linnean system, and illustrated with sixty plates, containing 260 figures of univalves and bivalves*. Booth, London, [i]–iv–[5]–7 +[1]–4 + [i]–ii–xxix–[xxx]–xxxi–xli–[xlii–xliii]–xliv–xlxix–[l–li]–lii–lxi + [1]–2–246 pp., 59 + 4* pls. [reprint of 1814–1815, with title page and p. 246 modified].

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Revised ms. accepted 3 December 2010

APPENDIX A
THE EDITIONS OF WOOD'S *INDEX TESTACEOLOGICUS*

The 1818 Edition vs. the 1823–1825 Edition

Pages [vii]–viii + 1–188 are identical in both editions. That the type was not reset can be demonstrated by numerous instances of broken typeface, as well as instances of missing type. Either the type was left standing for seven years and then a new printing made, or, more likely, fewer copies were sold in 1818 than expected, and the existing stock was issued with new first pages. That the 1823–1825 edition was issued in two parts was probably due to the plates not being ready, because the text certainly was.

1818 – [i–ii] (title page + blank verso)–[iii]–v (Preface + blank verso)–[vii]–viii (Abbreviations) + 1–188 pp., 8 pls., [2] pp. (Index, errata verso).

Some copies contain an addition leaf that is an advertisement for Burrow's *Elements of Shells*.

1823–1825 – [i–ii] (title page + blank verso)–[iii]–vi (Preface)–[vii]–xiv (A synopsis of the Linnean genera)–[xv]–xx (Lamarck's divisions of the Linnean genera, referred to the figures of the *Index Testaceologicus*), [xxi]–xxxii (List of subscribers & Advertisement) + [vii]–viii (Abbreviations; same as 1818) + 1–188 (A catalogue of shells; same as 1818) + [1]–4 [Lamarck's divisions of the Linnean genera*) + [i–ii] (Index generum/English index, recto; Errata, verso), 38 pls. [vii–viii +1–4 + 1–64, pls. 1–13, June 1823; i–xxxii + 65–188 + [ii] pp., pls. 14–38, 1825].

*In 1823, pp. [1]–4, "Lamarck's divisions of the Linnean genera, referred to the figures of the *Index testaceologicus*" covered the genera issued at that time. In 1825, these four pages were replaced by pages xv–xx listing all 35 genera. Referred to as "a temporary index" by Reynell (1918: 27), these four pages were not included in his collation and were described by Dance (1972: 161) as "preliminary matter … subsequently cancelled." These four pages are rare as most were discarded when they were replaced in 1825.

As previously, an advertisement for Burrow's *Elements of Shells* was appended. Some copies have a small slip bound in of "Subscribers omitted", issued in 1825 after the main list was printed. The "Abbreviations" pages [vii]–viii are not part of the i–xxxii page run, their pagination being unchanged from the 1818 edition.

The 1828a Edition

In 1828, the type was completely reset, although the wording is almost completely identical. The differences we have noticed are listed below. The size of the type was increased in 1828, and it was also printed on larger leaves. The plates remained unchanged.

1828a – [i–ii] (title page + blank verso)–[iii]–vi (Preface)–[vii]–xiv (A synopsis of the Linnean genera)–[xv]–xx (Lamarck's division of the Linnean genera…)–[xxi]–xxii (Abbreviations)–[xxiii–xxiv], (Directions to the binder + blank verso) + 1–212 pp., 38 pls.

Errors and Differences Between 1818/1823–1825 and 1828a Editions

In 1818, 1825 & 1828a there is an uncorrected error on p. 27: the reference for species 41, *Cardium rigidum*, should be figs. 2, 3; not 1, 2.

The text to the Preface is identical in the two editions, but in 1825, the text on p. vi occupies a full page, whereas in 1828 p. vi has only six lines of type.

Seven references were added to the "Abbreviations" pages [pp. xxi–xxii].

In 1828, following p. xxii, there is a single "Directions to the Binder" sheet [xxiii], which may not have been bound into some copies.

Throughout the 1828a edition, localities have, in many cases, been expanded [e.g., "South Seas" instead of "S. Seas"].

The following are the changes made in the list of species between the two editions:

page
5. First reference for *Lepas tintinnabulum* corrected from 285 to 385.
5. More "synonyms" (references) added to some species.
9. Species #12*, Pholas teredula*, omitted in 1828. There was no fig. 12 in 1823, but it was listed.
11. #17, *Mya dcussata* corrected to *decussata*.
13. #4, *Solen truncatus* incorrectly changed to *truncata*.
15. #26, *Solen biradiata* corrected to *biradiatus*.
40. #105, *Venus corrugata* changed to *obsoleta* with [*corrugata*] underneath.
53. Under *Ostrea vulsella* – [*Mya vulsella*] added.
62. #10 & #11, *Argonauta* omitted as discussed herein under *A. bullata*.
70. #37, *Conus leucostictos* – error made in 1828a in correcting *leucosticus* to *leucostictus*.
74. #102, *Conus monachus* changed to *C. puncticulatus*.
78. #155, *Conus geographicus* changed to *Conus geographus*.

108. #66, *Buccinum smaragdulus* changed to *B. rusticum*.
115. #166, *Buccinum imbricatum* is omitted in 1828a and the remaining 6 *Buccinum* are renumbered. There was no figure 166 in 1825 and in 1828 the figure numbers on the plate were changed to reflect the renumbering.
129, #111, *Murex amplustre* changed to *M. aplustre* in error.
140. #106, *Trochus inaequalis* changed to *T. gibberosus*.
150. #112, *Turbo albearia* changed to *T. alveare*; still an error for *T. alvearia* Dillwyn.
155. #13, *Helix algiri* changed to *H. algira*.
162. #97, *Helix lusitanica* changed to *lucitanica* in error.
164. #120, *Helix fasciatus* – [*Vivipara* var.] added under name.
176. #20, *Haliotis phyanotis* changed to *phymotis* – The errata page in 1825 had corrected it to *phimotis*.
180. #59, *Patella caeruleata* changed to *caerulea*.
186. #29, *Serpula cornu-copiae* – [*Helix*; untwisted] added in 1828a.

p. [189] in both editions is an "Index Generum. English Index" printed on recto only in 1828. In 1825, the verso of this page contained a list of errata. All but two of these were changed in 1828 (noted above among the changes):

page
124. #25, *lacerus* read *lacera* [not changed].
176, #20, *phyanotis* read *phimotis* [changed to *phymotis* instead, as noted above].

In 1828, an Index, not present in 1825, was added on pp. [191]–212. After this Index, a single sheet printed on both sides was added advertising books for sale by Wood, which may not be present in some bound copies.

APPENDIX B
THE HANLEY EDITIONS

In 1842 Hanley decided to issue an additional supplement to Wood's *Index Testaceologicus*. Hanley's supplement is difficult to describe as it was not completed until 1856 and evolved in the process. Also, in 1856, he published a "new and entirely revised" edition of Wood's *Index* including only the species and figures in Wood 1828a and 1828b with his own comments on synonymy added. Instead of a separate column for location of the specimens, Hanely utilized symbols that appear after the species names.

1842a–1843. [*An illustrated, enlarged, and English edition of Lamarck's species of shells, comprising the whole of the recent additions in Deshayes' last French edition, with numerous species not noticed by that naturalist: accompanied by accurate delineations of almost all the shells described, and forming the third edition of the Index Testaceologicus*, 1843] [W. Wood, London], 224 + 8 + [3] pp., 3 pls. [pp. 1–32, pls. 1–2, 1842; pp. 33–224, 8 (Systematic List), [3] (List of Illustrations), pl. 3, 1843].

No title page was issued for this work. The title listed is taken from Woodward (1922: 432) who had it in square brackets. The text of this work is incorporated in the following item but the three plates do not appear therein. This work is referred to by Hanley (1856a: v) as "*Lamarck's Species of Shells*." Hanley further stated that the publisher, William Wood, Jr., being dissatisfied with the plates, "discontinued the work which should contain 3 plates and 224 pages." The plates had been transferred from the original engravings to stone for lithographic printing with unsatisfactory results.

The eight page list is a "Systematic list of the shells illustrated in this work." The figures are all copies of previously published figures, with the origin stated for each. The figures are from Wood's *General Conchology* or *Index* and from Hanley's yet unissued plates ix–xiii. The latter plates had obviously been drawn, but they were published only later with the rest of the letterpress as described below.

At the end there is an additional eight page list, "A list of the species delineated in the supplementary plates of the descriptive and illustrative catalogue of shells." This is a list, by plates, of the species figured on Supplementary plates ix–xiii which had not yet been issued but includes all of the plates referenced in the text through page 224. These eight pages are not mentioned elsewhere. It is notable that these eight pages do not contain errors in numbering, etc., that are in the same list published for the completed 1842c–1846 version. That the correct pages were issued first may be determined by the fact that the final list for all 24 plates was set with wider spacing between listing to occupy more of the page. This is not an aberration; an identical copy is the library of the Academy of Natural Sciences of Philadelphia.

This work differs from Wood's format in that Hanley added descriptions of the species. He also added more recently described genera and species.

1842b–1846. *An illustrated and descriptive catalogue of recent shells, by Sylvanus Hanley, B.A., F.L.S. The plates forming a third edition of the Index Testaceologicus, by William Wood.* W. Wood, London, 272 + 8 + 18 pp., pls. 9–19.

There was no title page, this title being taken from a cover for "Pt. 1. Letterpress" in The Natural History Museum, London. It bears a space for a Part number, and 1 is written there on this copy. It is undated, with 1846 penciled in. Woodward (1922: 432) listed this "edition" with the 1842a–1843 listing above. Those pages are the same in this version but the three plates of that edition have been replaced by the Supplementary plates IX–XIX. According to Woodward, plates 9–13 were issued shortly after 1843, "pls. xiv–xvi about a year later, and pls. xvii–xix some two years later."

Listed by Woodward as a complete work but in view of the 10-year period between parts it is likely that the work to this stage was simply bundled and bound by some subscribers (as were similar parts of Reeve's *Initiamenta* which underwent a similar hiatus). There is a convenient break between pages 272–273 as 272 is the end of a signature, but the text on that page ends in the middle of a paragraph that continues onto page 273.

1842c–1856a. *An illustrated and descriptive catalogue of Recent bivalve shells.* London: Williams & Norgate, xviii + 392 + 24 pp., pls. 9–24. [1–32, 1842; 33–272, pls. 9–13, 1–8 (plate explanations for pls. 9–13), 1843; pls. 14–16, 1844; pls. 17–19, 1846; i–xviii, 273–392, pls. 20–24, 9–24 (plate explanations),1856].

Pages 1–224 of this work are identical to the work dated 1842–1843 (and probably pp. 225–272 also, but an example of the 1842b–1846 iteration is not available to us). Hanley's (1856a: v) description of the dates of printing are, like everything he wrote, difficult to understand. A single page "Books on Shells", provenance unknown as it lists one book published by Reeve as well as books published by Williams & Norgate, is tipped-in in the back of the copy of this Hanley volume at hand. It lists Hanley's 1855 *Ipsa Linnaei Conchylia.* About the work under discussion, the last item listed, it is stated that "This work, so long discontinued, is now resumed. Part IV of the Plates, containing 180 figures by Wood, to be published at Christmas." This informs us that Part IV must have been Plates 17–19, as every plate has 60 figures and Plates 20–24 have, of course, 300 figures. This cannot be reconciled with Hanley's statement indicating that the remaining text (pp. 273–392) appeared at one time and finished the work and his footnote (page vi) stating: "Plates 20–24, with their explanatory text, were published on the 26th of July last." The term "explanatory text" must refer to the plate captions. The only places the plate captions can be separated without overlap are between plates 13–14 and 21–22.

A paper by Reynell (1918) collating this work contains several errors. For 1843, he lists "pp. 1–144 + 7". This comes from Hanley's statement (1856a: v) that "Sheets B, C, were separately issued at the close of 1842, and conjointly … with the seven succeeding ones … "Reynell evidently took the "seven" to be pages, but they are signatures (Hanley's "sheets") to which Haley made reference. Signatures B and C, plus the next seven (D–K) add up to nine signatures which at 18 pages each gives the correct total of 144 pages. Where Reynell got Sheets "J–Q" is a mystery. An uncut copy at hand, which appears to be totally complete, contains no signature J. Signature Q falls nicely into Hanley's "Sheets L to S (p. 145 to 272)". Through signature T there are 16 pages per signature and later signatures have only 8 pages.

The title page, below the author's name and publications, is imprinted: "With 960 figures by Wood and Sowerby, forming an Appendix to the *Index Testaceologicus.*" The citation above lists the first eight pages of the plate explanations as published in 1843 but evidently new pages were issued in 1856 which contain errors not on the 1843 pages.

The Academy of Natural Sciences of Philadelphia holds Hanley's personal copy of this work described as:

> "It's marked on the flyleaf 'Hanley's own copy from his library. Geo. H. Clapp, PGHPA [Pittsburgh, PA]. Purchased in London, Nov. 1900'. Hanley had the whole work rebound with a folded sheet interleaved between each pair of pages, on which he wrote his comments and notes in pencil. These can

> be quite detailed comments about generic placements and references to other works, or just 'Type in my coll.' and 'Type in Mus.' There are hundreds if not thousands of them. Hanley also cut out all the figures from his plates and tipped them into the outer page margins, each alongside its relevant species entry. At the end of the book are a further 80 pages on which he cut and arranged hundreds of figures in a systematic order. These are all small monochrome engravings, but the Chitons and Barnacles are in color." – (Paul Callomon, personal communication, July 2010).

1856b. *Index testaceologicus, an illustrated catalogue of British and foreign shells, containing about 2800 figures accurately coloured after nature, by W. Wood, F.R.S., F.L.S. – A new and entirely revised edition, with ancient and modern appellations, synonyms, localities, etc. etc.* Willis and Sotheran, London, xx + 234 pp., 38 + 8 pls.

As mentioned, this is a reprint of the plates from Wood's 1828a and 1828b editions with Wood's column for "Linnean names" retained with same names and with the English names listed in a smaller font under them instead of in another column. The second column is leaded "Lamarckian genus" followed by a final column headed "Authority-Synonyms-Locality." Hanley added a number of synonymies and references that are sometimes helpful.

An example of Hanley's difficult style of writing, in which he seems to consider that his readers are endowed with some degree of clairvoyance, is the final paragraph of the Introduction to this work. Hanley stated:

> "The Appendix, which contains about 960 figures of species and genera not inserted in the original publication, is issued as a separate volume, the drawing being accompanied by a descriptive letter-press, expressly written to elucidate the bivalves delineated in the Index Testaceologicus." – Hanley (1856b: ii)

This is a reference to Hanley's 1842c–1856 "*Recent bivalve shells*", which is not mentioned by name in 1856b, was issued by a different publisher, and in which the word "*Appendix*" appears only on the lower part of the title page. A reader not already knowing of the other work would be quite puzzled at the intent of this paragraph.

APPENDIX C
INDEX TO WOOD AND "WOOD" TAXA

To facilitate locating Wood taxa, the following Index contains taxa made available by Wood in bold face and taxa incorrectly attributed to Wood in regular italics type (along with one generic misspelling by Wood). G indicates families of the Gastropoda; B indicates families of the Bivalvia. Taxa of the Polyplacophora and Cephalopoda are listed alphabetically without family breakdown. This index does not cover senior or junior synonyms or homonyms of Wood's taxa.

abbreviata, Nassa	G: Nassariidae
aculeatus, Murex	G: Muricidae
acuminatus, Conus	G: Conidae
acuminatus, Murex	G: Fasciolariidae
acuminatus, Trochus	G: Littorinidae
acuta, Tellina	B: Tellinidae
aequalis, Trochus	G: Trochidae
ajar, Chama	B: Carditidae
alata, Mactra	B: Mactridae
alata, Mya	B: Unionidae
alba, Mactra	B: Semelidae
alba, Tellina	B: Tellinidae
albearia, Turbo	G: Cerionidae
albidus, Trochus	G: Trochidae
albus, Trochus	G: Trochidae
alveare, Turbo	G: Cerionidae
amatum, Buccinum	see: *armatum, Buccinum*
ambigua, Patella	G: Fissurellidae
americana, Arca	B: Arcidae
amethystus, Solen	B: Psammobiidae
anglicus, Turbo	G: Lauriidae
angulata, Chama	B: Trapezidae
angulata, Helix	G: Planorbidae
angulata, Mya	B: Hyriidae
angulata, Patella	G: Siphonariidae
angulata, Voluta	G: Volutidae
aplustre, Murex	G: Fasciolariidae
armatum, Buccinum	G: Muricidae
armillatus, Trochus	G: Trochidae
articulatus, Trochus	G: Trochidae
asperrima, Ostrea	B: Pectinidae
atratus, Trochus	G: Trochidae
aurantius, Conus	G: Conidae
aurantius, Turbo	G: Annulariidae
aureola, Helix	G: Helicinidae
auriculata, Nerita	G: Neritidae
aurisvulpina, Voluta	G: Ferussacidae
auritus, Strombus	G: Thiaridae
australis, Chama	B: Carditidae

australis, Nerita	G: Neritidae
australis, Turbo	G: Ampullariidae
australis, Turbo	G: Epitoniidae
australis, Voluta	G: Costellariidae

badius, Trochus	G: Trochidae
balteus, Conus	G: Conidae
berrii, Venus	B: Veneridae
bicarinata, Bulla	G: Achatinidae
bicarinatus, Murex	G: Turridae
bicarinatus, Turbo	G: Littorinidae
biradiata, Donax	B: Donacidae
biradiata, Solen	B: Psammobiidae
bistriatus, Chiton	Polyplacophora
bitubercularis, Murex	G: Ranellidae
brevidentatum, Buccinum	G: Muricidae
brownii, Helix	G: Helicinidae
brunneus, Conus	G: Conidae
buccinoides, Cancellaria	G: Cancellariidae
bulbosum, Buccinum	G: Muricidae
bulbus, Buccinum	G: Pseudolividae
bulimoides, Turbo	G: Thiaridae
bullata, Argonauta	Cephalopoda
bulverii, Helix	G: Hygromiidae
byronensis, Strombus	G: Thiaridae
byronianus, Trochus	G: Trochidae
byronii, Helix	G: Achatinellidae

caerulea, Voluta	G: Olivellidae
caerulescens, Trochus	G: Trochidae
caffra, Nerita	G: Neritidae
calcaratus, Murex	G: Melongenidae
calcarea, Helix	G: Subulinidae
callosum, Buccinum	G: Nassariidae
callosus, Trochus	G: Trochidae
calyculus, Trochus	G: Trochidae
canalis, Nerita	G: Neritidae
cancellatus, Strombus	G: Strombidae
candida, Nerita	G: Naticidae
capensis, Chiton	Polyplacophora
carina, Helix	G: Helicidae
carinatus, Turbo	G: Pomatiidae
cariniferus, Murex	G: Fasciolariidae
cariosa, Nerita	G: Neritidae
cariosus, Murex	G: Muricidae
cariosus, Unio	B: Unionidae
carmichaelis, Chiton	Polyplacophora
cassida, Patella	G: Hipponicidae
Castalea	B: Hyriidae
castanea, Voluta	G: Marginellidae
castaneus, Chiton	Polyplacophora
castaneus, Mytilus	B: Mytilidae
castrensis, Solen	B: Solenidae
catus, Conus	G: Conidae
ceratus, Murex	G: Fasciolariidae

chemnitzii, Turbo	G: Annulariidae
childreni, Tellina	B: Lucinidae
childreni, Venus	B: Cyrenidae
chlorostoma, Buccinum	G: Ranellidae
chrysalis, Turbo	G: Clausiliidae
citreus, Spondylus	B: Spondylidae
citrinum, Cardium	B: Cardiidae
clandestina, Cypraea	G: Cypraeidae
clanguloides, Trochus	G: Trochidae
clangulus, Trochus	G: Trochidae
clelandi, Trochus	G: Trochidae
coarctatum, Buccinum	G: Tonnidae
colosseus, Murex	G: Melongenidae
columellaris, Voluta	G: Olividae
columna, Turbo	G: Annulariidae
columnaris, Lymnaea	G: Achatinidae
commixta, Cypraea	G: Cypraeidae
complanata, Arca	B: Arcidae
compressus, Turbo	G: Annulariidae
concamerata, Helix	G: Streptaxidae
concameratus, Trochus	G: Trochidae
conica, Helix	G: Ampullariidae
conica, Serpula	G: Vermetidae [or Annelida]
contracta, Voluta	G: Mitridae
convexa, Mya	B: Thraciidae
convexa, Tellina	B: Tellinidae
cordiformis, Tellina	B: Tellinidae
corneus, Solen	B: Solenidae
cornu, Argonauta	G: Capulidae
cornu, Helix	G: Acavidae
coronata, Voluta	G: Mitridae
corrugata, Haliotis	G: Haliotidae
corrugata, Voluta	G: Costellariidae
corrugatus, Turbo	G: Clausiliidae
costatus, Conus	G: Conidae
costellaris, Voluta	G: Mitridae
costularis, Murex	G: Muricidae
costulata, Venus	B: Veneridae
costulatus, Turbo	G: Clausiliidae
crassa, Mya	B: Unionidae
crassa, Voluta	G: Mitridae
crassicostata, Chama	B: Carditidae
crassilabrum, Buccinum	G: Buccinidae
crassus, Murex	G: Ranellidae
crassus, Turbo	G: Turbinidae
crepidularia, Nerita	G: Neritidae
cristatus, Murex	G: Muricidae
cruenta, Voluta	G: Olividae
crystallina, Patella	G: Fissurellidae
crystallina, Tellina	B: Tellinidae
curvirostris, Murex	G: Buccinidae
curvirostris, Murex	G: Cerithiidae
curvirostris, Pleurotoma	G: Turridae
cylindrica, Arca	B: Arcidae

cylindrus, Helix	G: Urocoptidae
cyprinoides, Venus	B: Cyrenidae
cyprinus, Mactra	B: Mactridae
damaoides, Venus	B: Veneridae
dama, Voluta	G: Olivellidae
decisa, Helix	G: Viviparidae
decussata, Bulla	G: Ficidae
decussata, Tellina	B: Semelidae
dentata, Anomia	Brachiopoda
dentata, Helix	G: Bulimulidae
dentata, Tellina	B: Tellinidae
dentata, Turbo	G: Trochidae
dentatum, Buccinum	G: Muricidae
denticulata, Mactra	B: Mesodesmatidae
denticulatum, Buccinum	G: Muricidae
dilatatus, Strombus	G: Strombidae
dissimilis, Helix	G: Viviparidae
distortum, Buccinum	G: Buccinide
dufresnii, Helix	G: Caryodidae
duplicata, Nerita	G: Naticidae
eburneus, Conus	G: Conidae
echinatus, Murex	G: Turridae
edentulus, Turbo	G: Pupillidae
elegans, Bulla	G: Bullidae
elegans, Murex	G: Turridae
elegans, Tellina	B: Tellinidae
elegans, Turbo	G: Annulariidae
elegans, Venus	B: Veneridae
elegantulus, Trochus	G: Trochidae
elongata, Arca	B: Iridinidae
elongatum, Buccinum	G: Terebridae
elongatus, Mytilus	B: Mytilidae
elongatus, Trochus	G: Trochidae
elongatus, Turbo	G: Annulariidae
erythrostoma, Voluta	G: Olividae
exalbida, Helix	G: Helicidae
exasperatus, Murex	G: Cerithiidae
exustus, Mytilus	B: Mytilidae
falcata, Pholas	B: Pholadidae
fascia, Turbo	G: Annulariidae
fasciatus, Chiton	Polyplacophora
fasciolata, Helix	G: Thiaridae
ferrugo, Murex	G: Muricidae
fibula, Helix	G: Helicidae
filosus, Trochus	G: Trochidae
filum, Voluta	G: Mitridae
fimbriatum, Cardium	B: Cardiidae
fimbriatus, Turbo	G: Epitoniidae
fissurata, Voluta	G: Mitridae
flammula, Voluta	G: Volutidae
flavidus, Turbo	G: Megalomastomatidae
floridus, Strombus	G: Strombidae
fluctuosus, Turbo	G: Turbinidae
fluviatilis, Helix	G: Pleuroceridae
foliaceus, Turbo	G: Cyclophoridae
foliatus, Murex	G: Muricidae
foliosum, Buccinum	G: Littorinidae
folium, Mytilus	B: Isognomonidae
formosa^{1}*, Helix*	G: Camaenidae
formosa^{2}***, Helix***	G: Helicidae
formosus, Trochus	G: Trochidae
formosus, Turbo	G: Urocoptidae
fragaria, Voluta	G: Buccinide
francesii, Turbo	G: Assimineidae
fraterna, Helix	G: Polygyridae
fulgurans, Buccinum	G: Buccinidae
fulvus, Chiton	Polyplacophora
fulvus, Turbo	G: Annulariidae
funiculus, Murex	G: Muricidae
funis, Turbo	G: Viviparidae
fuscata, Serpula	G: Vermetidae
fuscatus, Conus	G: Conidae
fuscescens, Helix	G: Vitrinidae
fuscus, Turbo	G. Ariculidae
galea, Strombus	G: Strombidae
gangraenosa, Cypraea	G: Cypraeidae
gemmulatum, Buccinum	G: Buccinidae
gigantea, Ostrea	B: Pectinidae
glabra, Nerita	G: Naticidae
glacialis, Arca	B: Yoldiidae
globosa, Mya	B: Myidae
goniostoma, Helix	G: Strophocheilidae
goodalli, Voluta	G: Marginellidae
gracilior, Strombus	G: Strombidae
gracilis, Conus	G: Conidae
gracilis, Turbo	G: Urocoptidae
gracilis, Voluta	G: Volutidae
gradatus, Conus	G: Conidae
granosa, Fasciolaria	G: Fasciolariidae
granosa, Helix	G: Pleurodontidae
granosus, Trochus	G: Trochidae
granulatus, Murex	G: Cerithiidae
granulatus, Strombus	G: Strombidae
gravis, Mya	B: Unionidae
gravis, Voluta	G: Turbinellidae
guadeloupensis, Helix	G: Orthalicidae
guinaicus, Conus	G: Conidae
guineensis, Solen	B: Solecurtidae
guttata, Voluta	G: Marginellidae
harpa, Buccinum	G: Harpidae
harpa, Voluta	G: Volutidae
haustrum, Argonauta	Cephalopida
helicella, Helix	G: Helicidae

hians, Venus	B: Veneridae
hiantula, Patella	G: Fissurellidae
hippocastanum, Murex	G: Muricidae
hystrix, Murex	G: Muricidae

icelandica, Venus	B: Arcticidae
ignea, Voluta	G: Costellariidae
imbricata, Arca	B: Arcidae
imbricata, Haliotis	G: Stomatellidae
imbricatum, Buccinum	G: Muricidae
imperialis, Bulla	G: Ovulidae
imperialis, Voluta	G: Volutidae
incisus, Strombus	G: Strombidae
incrassata, Chama	B: Carditidae
incrassata, Voluta	G: Olividae
indistinctus, Trochus	G: Trochidae
inflexus, Solen	B: Pharidae
interrupta, Tellina	B: Tellinidae
interruptus, Conus	G: Conidae
interruptus, Trochus	G: Trochidae
interstincta, Cypraea	G: Cypraeidae
intorta, Patella	G: Patellidae
intricata, Nerita	G: Naticidae

jamaicensis, Turbo	G: Neocyclotidae
jugosus, Strombus	G: Strombidae
junonia, Voluta	G: Volutidae
juvenilis, Venus	B: Veneridae

kingii, Helix	G: Placostylidae
kingii, Venus	B: Veneridae

labiosus, Murex	G: Ranellidae
labiosus, Strombus	G: Strombidae
labrosa, Helix	G: Enidae
lacerata, Arca	B: Arcidae
lacerus, Murex	G: Muricidae
lactea, Cypraea	G: Cypraeidae
lacustris, Nautilus	G: Planorbidae
laevigatum, Buccinum	G: Planaxidae
laevigatus, Mytilus	B: Mytilidae
laevipes, Helix	G: Ariophantidae
laevis, Helix	G: Partulidae
laevis, Tellina	B: Tellinidae
laevis, Trochus	G: Trochidae
laevis, Turbo	G: Cyclophoridae
laevissima, Helix	G: Thiaridae
lamellata, Venus	B: Veneridae
lamellosus, Turbo	G: Epitoniidae
lancellata, Pholas	P: Pholadidae
laqueare, Patella	G: Fissurellidae
lazarus, Chama	B: Chamidae
lens, Voluta	G: Mitridae
lepida, Bulla	G: Ovulidae
ligatus, Turbo	G: Helicidae

lincea, Turbo	G: Annulariidae
linearis, Solen	B: Solenidae
lineata, Bulla	G: Bullidae
lineata, Helix	G: Thiaridae
lineatus, Chiton	Polyplacophora
lineolatum, Buccinum	G: Nassariidae
lineolatus, Strombus	G: Thiaridae
lineolatus, Turbo	G: Phasianellidae
lingua, Murex	G: Muricidae
listerae, Carocolla	G: Camaenidae
listeri, Helix	G: Bulimulidae
listeri, Trochus	G: Trochidae
listeriana, Helix	G: Camaenidae
lividus, Solen	B: Psammobiidae
longicaudus, Murex	G: Fasciolariidae
lubeo, Trochus	G: Trochidae
lucidus, Conus	G: Conidae
ludus, Turbo	G: Turbinidae
lugubris, Voluta	G: Mitridae
lunulatus, Turbo	G: Cyclophoridae
lutea, Tellina	B: Tellinidae
luteolus, Chiton	Polyplacophora
lyriformis, Voluta	G: Volutidae

maculatus, Turbo	G: Diplommatinidae
maculosum, Cardium	B: Cardiidae
madagascariensis, Donax	B: Donacidae
madeirensis, Helix	G: Helicidae
magnus, Solen	P: Solenidae
margarita, Cypraea	G: Cypraeidae
marginata, Voluta	G: Marginellidae
marginatum, Buccinum	G: Olividae
marginellus, Turbo	G: Cyclophoridae
mariae, Haliotis	G: Haliotidae
martinii, Turbo	G: Epitoniidae
maugeri, Helix	G: Urocoptidae
maugeri, Trochus	G: Trochidae
maxima, Serpula	G: Vermetidae
maximus, Solen	B: Pharidae
mediterraneus, Trochus	G: Trochidae
mediterraneus, Turbo	G: Clausiliidae
melanopsis, Buccinum	G: Melanopsidae
melanostoma, Purpura	G: Buccinidae
meridionalis, Helix	G: Helicarionidae
micans, Voluta	G: Olividae
minimus, Turbo	G: Littorinidae
minus, Buccinum	G: Harpidae
mirabilis, Turbo	G: Annulariidae
mitra, Murex	G: Turridae
mitriforme, Cerithium	G: Cerithiidae
mitriformis, Murex	G: Turridae
modesta, Voluta	G: Volutidae
monodon, Helix	G: Polygyridae
montacuti, Trochus	G: Trochidae
montagui, Trochus	G: Trochidae

morbosus, Murex	G: Muricidae
morio, Mytilus	B: Pteriidae
mulus, Murex	G: Ranellidae
muricata, Tellina	B: Lucinidae
muricata, Voluta	G: Turbinellidae
muricatus, Turbo	G: Littorinidae
muscosa, Ostrea	B: Pectinidae

namocanus, Conus	G: Conidae
nasuta, Mya	B: Unionidae
nebulosus, Chiton	Polyplacophora
niger, Turbo	G: Turbinidae
nigrescens, Helix	G: Pleurodontidae
nivea, Cypraea	G: Cypraeidae
nivea, Tellina	B: Tellinidae
nodosa, Arca	B: Arcidae
nodosum Buccinum	G: Buccinidae
nodulosa, Mya	B: Unionidae
nodulosus, Turbo	G: Trochidae
norwegicum, Buccinum	G: Buccinidae
noveboracensis, Buccinum	G: Nassariidae
nux, Voluta	G: Olivellidae

obliqua, Mya	B: Unionidae
obliqua, Tellina	B: Semelidae
obliquata, Arca	B: Arcidae
oblongata, Mya	B: Unionidae
obscurus, Trochus	G: Trochidae
ochroleuca, Tellina	B: Tellinidae
odontis, Trochus	G: Trochidae
oculuscapti, Cyclophorus	G: Cyclophoridae
odontostoma, Helix	G: Orthalicidae
olivaceus, Trochus	G: Turbinidae
orbiculata, Helix	G: Camaenidae
orbiculatus, Solen	B: Pharidae
ornata, Nerita	G: Neritidae
ornata, Ostrea	B: Pectinidae
ornata, Venus	B: Veneridae
oryza, Voluta	G: Olividae
ostreoides, Anomia	Brachiopoda
ovata, Iridina	B: Iridinidae
ovata, Mactra	B: Mesodesmatidae
ovum, Pholas	B: Pholadidae
oweniana, Nerita	G: Neritidae
owenii, Nerita	G: Neritidae

papilla, Murex	G: Ranellidae
parthenopsus, Murex	G: Ranellidae
patula, Helix	G: Succineidae
patula, Nerita	G: Naticidae
pecteniforme, Cardium	B: Cardiidae
pectinata, Bulla	G: Philinidae
pectiniformis, Arca	B: Glycymerididae
pectunculus, Chama	P: Carditidae
pellisserpentis, Trochus	G: Trochidae
penitaria, Littorina	G: Littorinidae
perdix, Turbo	G: Phasianellidae
persicus, Strombus	G: Strombidae
peruviana, Voluta	G: Olividae
petiveriana, Helix	G: Urocoptidae
petiverianus, Turbo	G: Cyclophoridae
petrosus, Strombus	G: Cerithiidae
peziza, Patella	G: Calyptraeidae
phyanotis, Haliotis	G: Stomatellidae
picea, Mya	B: Hiatellidae
pictus, Murex	G: Cerithiidae
pictus, Trochus	G: Trochidae
pinnatus, Murex	G: Muricidae
pintado, Turbo	G: Littorinidae
planaxis, Buccinum	G: Planaxidae
planorbula, Helix	G: Cyclophoridae
planulata, Haliotis	G: Stomatellidae
pleurotoma, Murex	G: Turridae
plicata, Helix	G: Camaenidae
plicatus, Murex	G: Muricidae
plumbea, Nerita	G: Naticidae
poculum, Patella	G: Calyptraeidae
politus, Solen	B: Pharidae
portosanctana, Helix	G: Helicidae
praelonga, Mya	B: Unionidae
priamus, Bulla	G: Bullidae
principalis, Turbo	G: Epitoniidae
pulchella, Nerita	G: Neritidae
pulcher, Turbo	G: Annulariidae
pulcherrimus, Trochus	G: Trochidae
pulchra, Helix	G: Enidae
pulchra, Venus	B: Veneridae
punctata, Voluta	G: Volutidae
punctulata Helix	G: Helicidae
pusillus, Conus	G: Conidae
pyramidalis, Conus	G: Conidae
pyramis, Voluta	G: Mitridae
pyrum, Bulla	G: Bullidae

quadricostatus, Trochus	G: Trochidae
quadrimaculata, Cypraea	G: Cypraeidae

radiatum, Buccinum	G: Mitridae
raricostatus, Turbo	G: Epitoniidae
recens, Venus	B: Veneridae
recurva, Mactra	B: Mactridae
recurvirostrum, Cassis	G: Tonnidae
regius, Murex	G: Muricidae
reticularis, Trochus	G: Trochidae
reticulata, Venus	B: Veneridae
reticulatus, Conus	G: Conidae
reticulatus, Trochus	G: Trochidae
rigida, Mya	B: Unionidae
rigida, Voluta	G: Costellariidae
rigidum, Cardium	B: Cardiidae

rigidus, Murex	G: Fasciolariidae
ringens, Buccinum	G: Tonnidae
ringens, Cardium	B: Cardiidae
rosea, Anomia	Brachiopoda
rosea, Cypraea	G: Triviidae
rosea, Serpula	G: Vermetidae [or Annelida]
roseum, Buccinum	G: Harpidae
roseus, Conus	G: Conidae
rostrata, Chama	B: Trapezidae
rostrum, Arca	B: Iridinidae
rotunda, Mya	B: Unionidae
rubra, Anomia	Brachiopoda
rudis, Nerita	G: Neritidae
rudolphi, Buccinum	G: Muricidae
rufescens, Turbo	G: Barleeidae
rugosus, Strombus	G: Cerithiidae
rugosus, Trochus	G: Littorinidae
rugulosa, Mya	B: Unionidae
salmo, Murex	G: Fasciolariidae
sanguinea, Tellina	B: Tellinidae
sanguineus, Murex	G: Fasciolariidae
saxosus, Turbo	G: Turbinidae
sayii, Helix	G: Polygyridae
sayii, Strombus	G: Pleuroceridae
scabra, Helix	G: Helicidae
scabra, Ostrea	B: Limidae
scabra, Tellina	B: Lucinidae
scitula, Helix	G: Helicinidae
scobinata, Helix	G: Orthalicidae
scutellata, Patella	G: Calyptraeidae
semiconica, Nerita	G: Neritidae
semiglobusus, Murex	G: Muricidae
semigranosum, Buccinum	G: Tonnidae
septemvolva, Helix	G: Polygyridae
serpentina, Voluta	G: Mitridae
setosus, Chiton	Polyplacophora
sexradiata, Donax	B: Donacidae
siculus, Chiton	Polyplacophora
similis, Mactra	B: Mactridae
similis, Venus	B: Cyrenidae
sinistralis, Murex	G: Fasciolariidae
sinistrorsa, Helix	G: Dorcasiidae
smithii, Nerita	G: Neritidae
smithii, Trochus	G: Trochidae
soleniforme, Cardium	B: Cardiidae
soror, Helix	G: Camaenidae
spinosa, Nerita	G: Neritidae
squamosa, Arca	B: Arcidae
squamosa, Helix	G: Helminthoglyptidae
stutchburii, Venus	B: Veneridae
subauriculata, Ostrea	B: Limidae
subcarinata, Helix	G: Viviparidae
subglobosus, Murex	G: Muricidae
subplicata, Mactra	B: Mactridae
subrostratum, Buccinum	G: Buccinidae
subrugosa, Venus	B: Veneridae
subtriangulata, Mactra	B: Mesodesmatidae
sulcata, Chama	B: Carditidae
sulcata, Tellina	B: Tellinidae
sulcatus, Chiton	Polyplacophora
sulcatus, Trochus	G: Trochidae
sulcifera, Haliotis	G: Stomatellidae
sulculata, Helix	G: Thiaridae
suturalis, Turbo	G: Epitoniidae
taeniata, Voluta	G: Costellariidae
taeniatus, Conus	G: Conidae
taeniatus, Trochus	G: Trochidae
tankervillii, Buccinum	G: Olividae
tankervillii, Trochus	G: Helicinidae
tankervillii, Venericardia	B: Carditidae
taprobanensis, Mactra	B: Mesodesmatidae
tectiformis, Helix	G: Helicidae
tectum, Buccinum	G: Muricidae
tegula, Ostrea	B: Pectinidae
tellinoides, Arca	B: Nuculanidae
tenebrosa, Voluta	G: Olividae
tenera, Mactra	B: Mactridae
tenue, Buccinum	G: Tonnidae
tenuis, Solen	B: Solecurtidae
terpsichore, Buccinum	G: Columbellidae
tessellata, Cypraea	G: Cypraeidae
tessellata, Voluta	G: Marginellidae
tessellatum, Buccinum	G: Tonnidae
tessellatus, Chiton	Polyplacophora
tessellatus, Conus	G: Conidae
tigrina, Voluta	G: Olividae
torticollis, Turbo	G: Clausiliidae
tortus, Turbo	G: Megalomastatidae
tricostata, Haliotis	G: Haliotidae
tridentata, Helix	G: Polygyridae
tripolitana, Helix	G: Helicidae
trochlea, Trochus	G: Trochidae
truncata, Solen	B: Solenidae
truncatulus, Turbo	G: Clausiliidae
tuberculata, Littorina	G: Littorinidae
tuberculatus, Turbo	G: Littorinidae
tunicatus, Chiton	Polyplacophora
turbinatus, Trochus	G: Trochidae
turgidula, Helix	G: Helicidae
turris, Buccinum	G: Nassariidae
turritella, Turbo	G: Turritellidae
undata, Helix	G: Achatinidae
undosus, Trochus	G: Turbinidae
undulatus, Mya	B: Unionidae

unguis, Trochus	G: Turbinidae
unicarinatus, Turbo	G: Pomatiopsidae
unicornus, Strombus	G: Strombidae
unifasciale, Buccinum	G: Muricidae
unifasciata, Voluta	G: Costellariidae
unifasciatus, Murex	G: Fasciolariidae
valvatus, Cyclostoma	G: Cyclostomatidae
varicosus, Turbo	G: Epitoniidae
variegatus, Solen	B: Psammobiidae
varius, Turbo	G: Phasianellidae
veneriformis, Mactra	B: Astartidae
ventricosa, Bulla	G: Olividae
ventricosus, Orthostylus	G: Bradybaenidae
verrucosum, Buccinum	G: Nassariidae
vexillum, Helix	G: Orthalicidae
virginea, Helix	G: Pleuroceridae
viridis, Trochus	G: Trochidae
vittata, Voluta	G: Costellariidae
volvulus, Helix	G: Cyclophoridae
zebra, Buccinum	G: Columbellidae
zebra, Trochus	G: Trochidae
zebra, Turbo	G: Littorinidae
zonata, Voluta	G: Mitridae
zonatus, Trochus	G: Trochidae
zonatus, Strombus	G: Cerithiidae
zonula, Helix	G: Camaenidae

MALACOLOGIA, 2011, 54(1–2): 77–85

TYPE MATERIAL OF BIVALVE MOLLUSKS COLLECTED DURING *VÉNUS* VOYAGE (1836–1839) FROM KAMCHATKA, RUSSIA, IN THE MUSÉUM NATIONAL D'HISTOIRE NATURELLE, PARIS

Konstantin A. Lutaenko[1]* & Virginie Héros[2]

ABSTRACT

Syntypes of four species of bivalve molluscs – *Nucula laternaria* Valenciennes, 1846; *Nucula amygdalea* Valenciennes, 1846; and *Nucula oeolica* Valenciennes, 1846, all Yoldiidae; and *Cardium californiense* Deshayes, 1839, Cardiidae – collected from Kamchatka during the historic voyage of the *Vénus* (1836–1839), are illustrated and their taxonomic status and distribution are discussed.

Key words: Bivalvia, syntypes, Yoldiidae, Cardiidae, Kamchatka.

INTRODUCTION

The frigate *Vénus* was sent to the Pacific Ocean by the French government in 1836 to compile maps of bays and islands and to do geophysical and astronomical studies, to collect natural history objects, and to report on the whale fisheries in the Pacific for the benefit of the French industry (Buck, 1953; Chamberlin, 1960). The voyage commenced on December 29, 1836, from Brest, lasted for 30 months, and the ship sailed around the world. Captain Abel Du Petit-Thouars and his first officer, Chiron, collected almost 400 species and over 1,500 specimens of mollusks eventually deposited in the Muséum National d'Histoire Naturelle, Paris (Chamberlin, 1960; hereafter, MNHN). The famous French zoologist Achille Valenciennes** published 27 plates with illustrations of about 86 species of molluscs collected on the voyage. The images were accompanied by Latin names in the captions (at least 62 new names – Chamberlin, 1960), but the text never appeared (Dance, 1966). Most of the molluscs figured represented shallow-water species from the Indo-Pacific and the west coast of the Americas, but some were from the northwest Pacific; type material is identified in the collections of the MNHN (Lamy, 1922). From August 30 to September 15, 1837, the *Vénus* visited Avacha [Awatscha] Bay [Avachinsky Zaliv] in Kamchatka, now part of Russia, and then sailed for California. We identified type material of four species described from Kamchatka by Valenciennes and Deshayes (Deshayes, 1839; Valenciennes, 1846) in the collection of the MNHN; two of them appear to be long forgotten in the 20th century, one with unresolved taxonomic problems, and one was never figured. Deshayes (1839) described two additional species from Kamchatka – *Anomia macrochisma* Deshayes, 1839 and *Modiola cultellus* Deshayes, 1839 – but the type material was not found at the MNHN.

It is of interest that Valenciennes published two additional, frequently overlooked papers on molluscs of the northern Sea of Japan, collected by surgeon Barthe of the frigate *La Sybille* (Valenciennes, 1858a, b). These included descriptions of the bivalves *Pecten dominicanus* Valenciennes, 1858 (possible synonym of *Mizuhopecten yessoensis* (Jay, 1856); type material not found), *Mytilus unguiculatus* Valenciennes, 1858 (senior synonym of *Mytilus coruscus* Gould, 1861), and *Mactra sybillae* Valenciennes, 1858 (senior synonym of the well-known *Spisula sachalinensis* (Schrenck, 1862)). These were not illustrated, and only discovery of the type material (Habe, 1978; Kantor & Sysoev, 2002) allowed recognition of *M. sybillae* (supressed: Kafanov, 1983; Melville, 1985) and to qualify *M. coruscus* as a *nomen protectum* (Lutaenko, 2005b).

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[1] A. V. Zhirmunsky Institute of Marine Biology, Far East Branch of the Russian Academy of Sciences, Palchevskogo Str. 17, Vladivostok 690041, Russia

[2] Muséum National d'Histoire Naturelle, 55 Rue Buffon, 75231 Paris, France

* Corresponding author: lutaenko@mail.primorye.ru

**A. Valenciennes (1794–1865) was a French zoologist who made significant contribution to ichtyology; he worked with Georges Cuvier on the famous *Histoire naturelle des poissons* (1828–1848). See his biography: Monod et al. (1967), Bauchot et al. (1990).

Abbreviations

The following abbreviations are used in the paper: BMNH – The Natural History Museum, London; ICZN – International Code of Zoological Nomenclature; MNHN – Muséum National d'Histoire Naturelle, Paris; USNM – National Museum of Natural History; Smithsonian Institution; Washington, D.C.

LIST OF SYNTYPES

Family Yoldiidae Dall, 1908

Nucula laternaria Valenciennes, 1846 (Figs. 1C, 3A, B)

Present status: junior synonym of *Megayoldia thraciaeformis* (Storer, 1838). Original description/Illustration: Valenciennes, 1846: pl. 23, fig. 5.

Type locality: Kamchatka. Type material: 1 syntype (complete shell), MNHN 21937, length 40.8 mm, height 25.7 mm.

Comments

The type specimen is represented by two valves glued to a piece of cardboard found in the general collection in 2004. The original label glued to the opposite side of the cardboard mount states (Fig. 2A): "Soft part in alcohol under the letter A, gift from M. Neboux Voyage de la Vénus" (Adolphe Simon Neboux, 1806–1844, was a doctor and naturalist on board the *Vénus*). The original figure (Valenciennes, 1846: pl. 23, fig. 5; Fig. 1C herein) corresponds well with the type specimen. According to Coan et al. (2000) and Warén (1989), *M. thraciaeformis* has at least eight synonyms – *Nucula navicularis* Couthouy, 1839; *Yoldia angilaris* Möller, 1842; *Yoldia regularis* Verrill, 1884; *Portlandia dalli* Krause, 1885; *Nucula groenlandica* Posselt, 1898; *Yoldia secunda* Dall, 1916; *Yoldia scapha* Yokoyama,

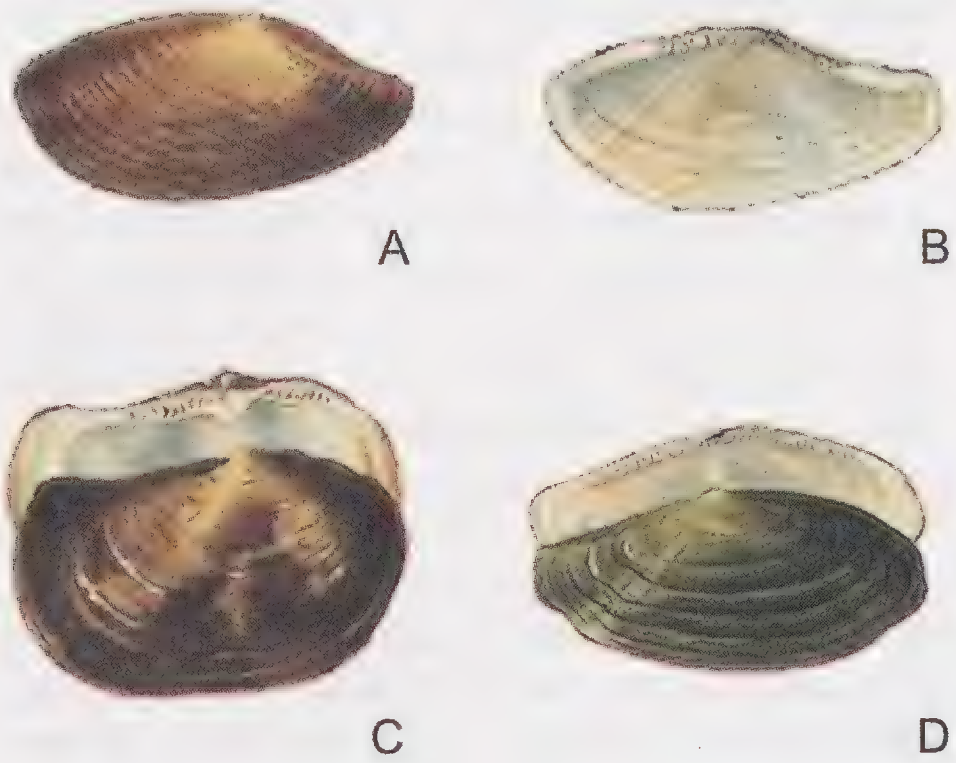
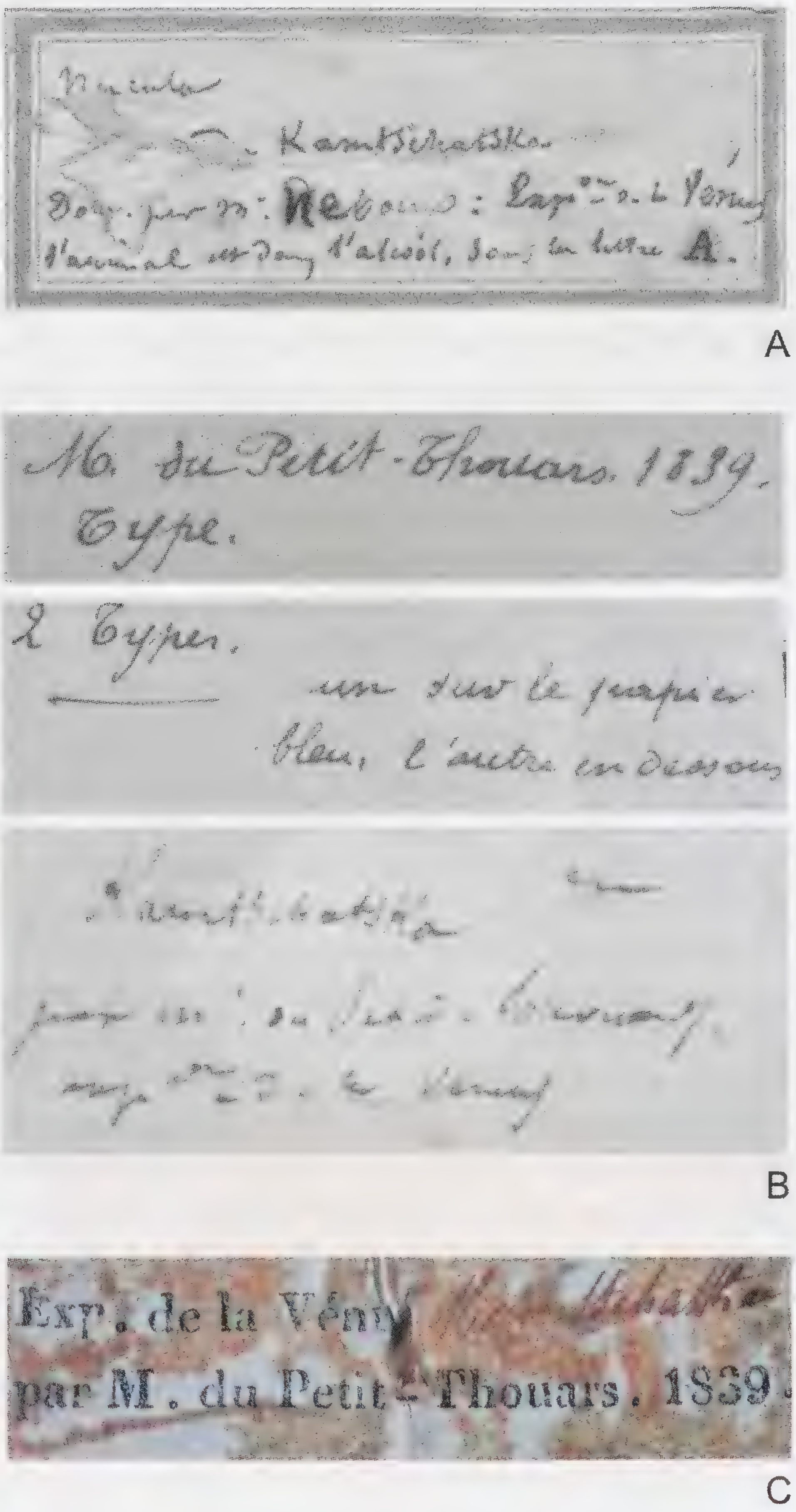


FIG. 1. Original illustrations of the bivalve species described from Kamchatka and collected by *Vénus* voyage in 1837. A, B: *Nucula aeolica* Valenciennes, 1846 (Valenciennes, 1846, pl. 23, fig. 3); C: *Nucula laternaria* Valenciennes, 1846 (Valenciennes, 1846, pl. 23, fig. 5); D: *Nucula amygdalea* Valenciennes, 1846 (Valenciennes, 1846, pl. 23, fig. 6).



M. du Petit-Thouars. 1839.
Type.

2 Types.
un sur le papier
bleu, l'autre en dessous

Exp. de la Vén
par M. du Petit-Thouars. 1839.

FIG. 2. Original museum labels for the type lots of the three species in the NMHN. A: *Nucula laternaria* Valenciennes, 1846; B: *Nucula amygdalea* Valenciennes, 1846; C: *Cardium californiense* Deshayes, 1839.

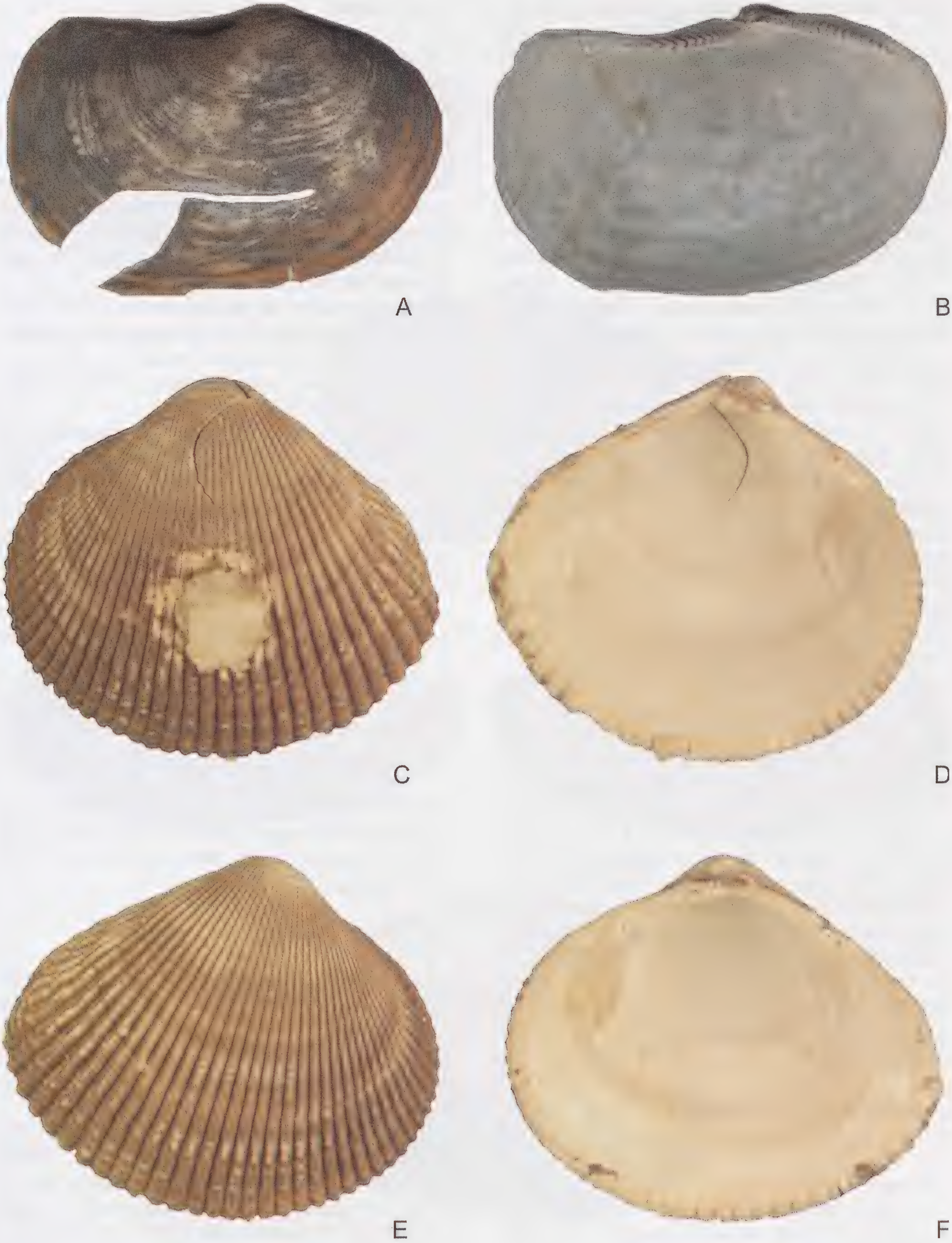


FIG. 3A, B. *Nucula laternaria* Valenciennes, 1846 (= *Megayoldia thraciaeformis* (Storer, 1838)). Syntype, right (A) and left (B) valves of complete shell, MNHN 21937, length 40.8 mm, Loc. Kamchatka; C–F: *Cardium californiense* Deshayes, 1839 (= *Clinocardium* (*Keenocardium*) *californiense* (Deshayes, 1839)). Syntype MNHN 3970, left (C, D) and right (E, F) outside and inside, length 62.5 mm, Loc. Kamchatka. [Since this photo was taken in 2004, the left valve (C, D) was broken].

1926; *Microyoldia ochotensis* Scarlato, 1981) – but *N. laternaria* was not considered by these authors. However, in the 19th century, Hanley (1860: 167) listed *Y. laternaria* as a synonym of *Leda thraciaeformis* (in the sect. II – subgenus *Yoldia*), which was followed by G.B. Sowerby II (1871). It is very likely that *Microyoldia ochotensis* Scarlato, 1981, described from a single specimen from 43 m in the southern Sea of Okhotsk, is a young specimen of a North Pacific species of *Megayoldia. Megayoldia ochotensis* lacks a ligament pit characteristic of young specimens of *M. thraciaeformis* (Warén, 1989). *Megayoldia kamtchatkana* Scarlato, 1981, described from off Avacha Bay, southeastern Kamchatka, and living at 1,500–2,000 m, is a synonym of *Megayoldia montereyensis* (Dall, 1893) (Coan et al., 2000). *Megayoldia martyria* (Dall, 1897) and *Megayoldia lischkei* (E. A. Smith, 1895) from the North Pacific both differ from *M. thraciaeformis* in the shell shape: elongate-subquadrate, with posterior end longer and bluntly pointed in the former species, and more produced, but not clearly truncate posterior end in the latter species. Amano (1996) regarded *M. lischkei* as belonging to the genus *Portlandia* Mörch, 1857.

Megayoldia thraciaeformis is widely distributed in the low Arctic Ocean and circumboreally, south to off San Francisco Bay, California, along the American coast of the Pacific Ocean (Coan et al., 2000), and to Japan (Higo et al., 1999) and Korea (Kwon et al., 2001; Min et al., 2004). In Russian waters, it is known in the Sea of Japan south to Possjet Bay, the Sea of Okhotsk, southeastern Kamchatka, and the Bering Sea (Scarlato, 1981). The known depth range is 20–545 m in Russian part of the Pacific Ocean (Scarlato, 1981), and 25–760 m for the entire Pacific (Coan et al., 2000). In the Atlantic Ocean, it is distributed as far south as southern Greenland and Massachusetts Bay (Warén, 1989).

Nucula amygdalea Valenciennes, 1846

(Figs. 1D, 4D)

Present status: junior synonym of *Yoldia* (*Yoldia*) *hyperborea* (Gould, 1841). Original description/illustration: Valenciennes, 1846: pl. 23, fig. 6.

Type locality: Kamchatka. Type material: 2 syntypes (complete shells; two valves are damaged), MNHN 21938, 1st specimen: length 47.6 mm, height 22.0 mm; 2nd specimen: length 38.5 mm, height 17.8 mm.

Comments

Subgenus *Yoldia* (*Yoldia*) Möller, 1842, is characterized by the absence of sculpture, or a few commarginal lirae, whereas two other North Pacific subgenera – *Yoldia* (*Cnesterium*) Dall, 1838, and *Yoldia* (*Kalayoldia*) Grant & Gale, 1931, have either oblique striae or sharp commarginal ribs. Based on this feature, the syntypes of *N. amygdalea* undoubtedly belong in *Yoldia* (*Yoldia*), and differ from *Yoldia* (*Yoldia*) *myalis* (Couthouy, 1838), the allied species of the subgenus in the North Pacific. Coan et al. (2000) suggested that *Yoldia bartschi* Scarlato, 1981 (= *Yoldia tartarica* Bartsch in Ushakov, 1953, *nom. nud.* – see Ushakov, 1953, p. 261) is a synonym of *Y. hyperborea.*

There has been continuing discussion on the relationship between *Y. hyperborea* and *Y. amygdalea* (Cowan, 1968; Bernard, 1979; Scarlato, 1981), but it seems that *Y. hyperborea* is a pan-Arctic, amphi-Pacific and North Atlantic (south to Norway, Iceland and Greenland) species (Coan et al., 2000).

Nucula oeolica Valenciennes, 1846

(Figs. 1A, B, 4A–C)

Present status: unclear; see below. Original description/illustration: Valenciennes, 1846: pl. 23, fig. 3.

Type locality: Kamchatka. Type material: 1 syntype (damaged shell), MNHN 21939, size of the most complete right valve: length 30.8 mm, height 17.1 mm.

Comments

This species was forgotten in the 20th century. However, *N. oeolica* was cited by Hanley (1860), G. B. Sowerby II (1871), Schrenck (1867), and Paetel (1890) as a synonym of *Yoldia lanceolata* (J. Sowerby, 1817), a Pliocene-Pleistocene European species.

Nucula oeolica undoubtedly belongs to the subgenus *Yoldia* (*Cnesterium*) Dall, 1898, which is taxonomy complicated. There are at least ten available names regarded as synonyms of the boreal-arctic *Yoldia* (*Cnesterium*) *seminuda* Dall, 1871, complex, and among them six names refer to Recent species (Coan et al., 2000): *Y. seminuda*, *Y. scissurata* Dall, 1897 (*nom. nov.* pro *Nucula arctica* Broderip & G. B. Sowerby I, 1829, *non* Gray, 1824); *Yoldia ensifera* Dall, 1897; *Yoldia keppeliana* G. B. Sowerby III, 1904; *Yoldia ensifera plena*

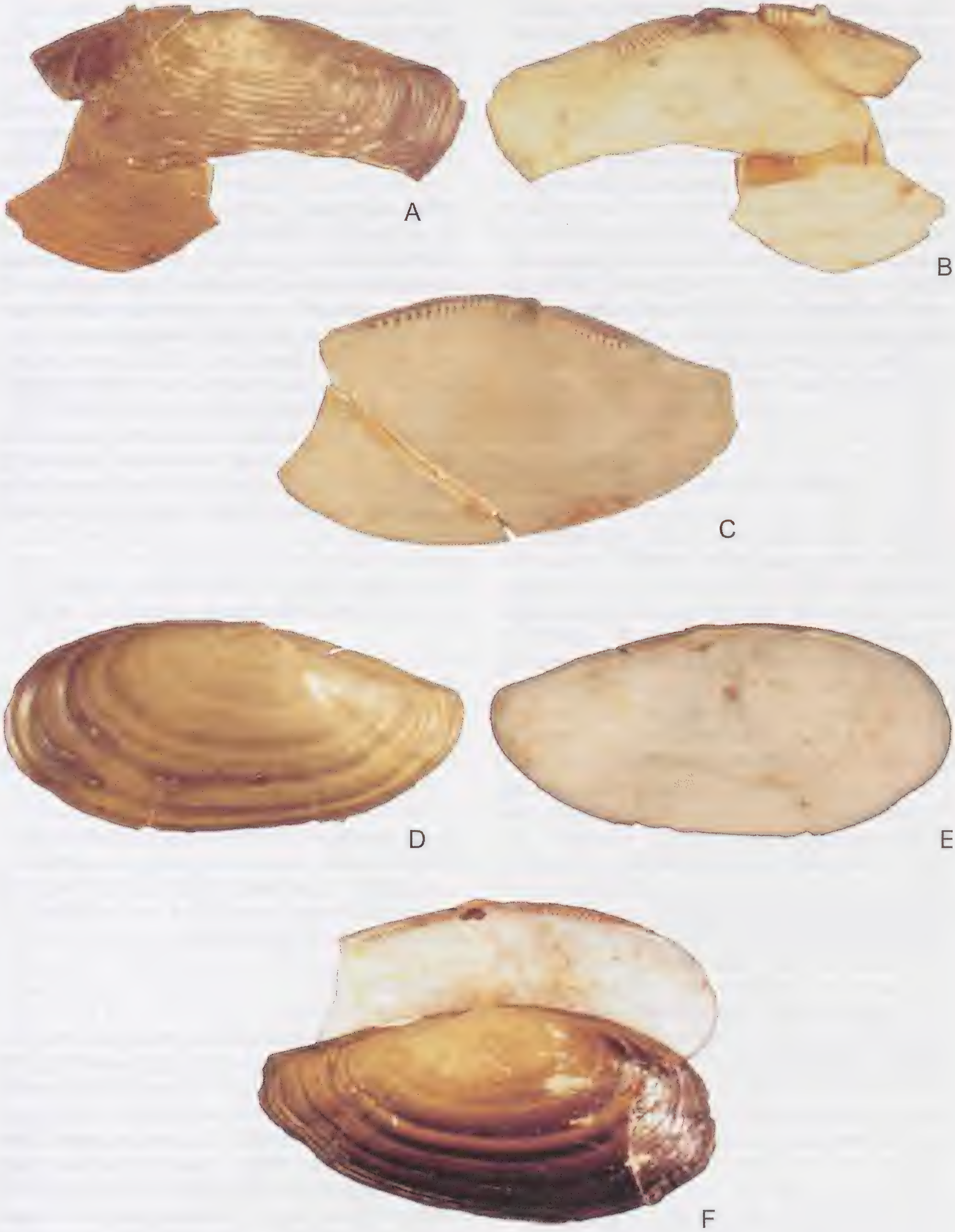


FIG. 4. *Nucula* sp. A–C: *Nucula aeolica* Valenciennes, 1846 (= *Yoldia oeolica* (Valenciennes, 1846)); A, B: Syntype MNHN 21939 left valve inside and outside; C: Syntype MNHN 21939 right valve outside, length 30.8 mm, Loc. Kamchatka; D, E: *Nucula amygdalea* Valenciennes, 1846 (= *Yoldia* (*Yoldia*) *hyperborea* (Gould, 1841)); D: Syntype MNHN 21938 left valve outside; E: Syntype MNHN 21938 right valve inside, length 38.5 mm, Loc. Kamchatka; F: *Nucula amygdalea* Valenciennes, 1846 (= *Yoldia* (*Yoldia*) *hyperborea* (Gould, 1841)), Syntype MNHN 21938, left valve outside and right valve inside, length 47.6 mm, Loc. Kamchatka.

Dall, 1908; and *Yoldia* (*Cnesterium*) *johanni* Dall, 1925. The relationships among these taxa are much in need of detailed study. Two other Recent species from the northwestern Pacific – *Yoldia* (*Cnesterium*) *toporoki* Scarlato, 1981, distributed in the southern Sea of Okhotsk and northern Sea of Japan (Scarlato, 1981; Lutaenko, 2002, 2005a), and *Yoldia* (*Cnesterium*) *notabilis* Yokoyama, 1922 (with a synonym *Yoldia excavata* Dall, 1925), distributed off Japan, Korea and northern China (Higo et al., 1999; Min et al., 2004; Xu & Zhang, 2008), are distinct representatives of the subgenus in that part of the Pacific Ocean.

Based on the examination of type specimens and illustrations of types of *Y. keppeliana* (2 syntypes, BMNH 1904.12.23.154 and 1904.12.23.155, 1 syntype MNHN 23246), *N. arctica* (1 figured syntype BMNH 1858.5.12.241), *Y. excavata* (syntypes USNM 249337; figured by Matsukuma et al., 1991: fig. 4A, B, and Higo et al., 2001: fig. B30s), *Y. johanni* (syntypes USNM 107694, figured by Matsukuma et al., 1991: fig. 4C, D, and Higo et al., 2001: fig. B31), *Y. notabilis* (lectotype figured by Oyama, 1980: pl. 21, fig. 5), *Y. seminuda* (holotype USNM 197678, figured by Moore, 1983: pl. 4, fig. 19) and *Yoldia* (*Cnesterium*) *pseudonotabile* Scarlato, 1981 (holotype figured by Scarlato, 1981: photo 132), we can preliminarily assume that: (1) *Y. keppeliana* and *Y. johanni* are distinct from each other and are not identical to *Y. seminuda*; (2) *Y. keppeliana pseudonotabile* is a synonym of *Y. johanni*, and not of *Y. keppeliana* or *Y. notabilis*, as stated by Kafanov (1991); (3) *Y. notabilis* does not inhabit the Russian part of the Sea of Japan, and previous records (Lutaenko, 1999, 2002, 2005) are erroneous and may refer to *Y. seminuda*; (4) *Y. excavata* is a synonym of Y. *notabilis*, but not of *Y. seminuda* as stated by Scarlato (1981) and Kafanov (1991); and (5) *Y. oeolica* is the earliest available name for *Y. seminuda*.

It is of interest that *N. arctica* was described from “Oceano Arctico” but with indication that “two or three specimens were obtained in Vatcha Bay, Kamtschatka” (Broderip & Sowerby I, 1829), that is, Avacha Bay [Avachinsky Zaliv], because the bay was visited by the Blossom expedition in 1825–1828 under the command of Captain Beechey (Rosewater, 1968). Comparison of the original illustrations of Broderip & Sowerby I (1829: pl. 9, fig. 1), Valenciennes (1846: pl. 23, fig. 3) and type specimens clearly proves the conspecificity of *N. arctica* (= *Y. scissurata*) and *N. oeolica*.

Considering that *Y. oeolica* is a valid name that has priority over *Y. seminuda*, one may wish to apply the reversal of precedence in accordance with ICZN *Code* Article 23.9.1, which states that prevailing usage of *Y. seminuda* must be maintained when the senior synonym has not been used as a valid name after 1899 and the junior synonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years. However, some Japanese and Russian authors regard two other allied species, *Y. johanni* and *Y. keppeliana*, as separate distinct species, whereas Coan et al. (2000) thought that they might be synonyms of *Y. seminuda*. In any case, *Y. oeolica* has priority over these species as well. Until a detailed revision of *Yoldia* (*Cnesterium*) is undertaken, we prefer not to take any action with regard to this name at present.

Family Cardiidae Lamarck, 1809
Cardium californiense Deshayes, 1839
(Fig. 1C–F)

Present status: *Clinocardium* (*Keenocardium*) *californiense* (Deshayes, 1839) (Coan et al., 2000) or *Keenocardium californiense* (Deshayes, 1839) (Kafanov, 1999). Original description: Deshayes, 1839: 360.

Type locality: “Côtes de Californie” (error = Kamchatka; see below). Type material: 2 syntypes (complete shells), MNHN 3970 (figured here), length 62.5 mm, height 54.7 mm, width 34.3 mm; MNHN 3971.

Comments

Kafanov (1999) mentioned two specimens as “syntypes” in the collection of the MNHN with reference to letters of E. Fischer-Piette and A. M. Keen. Earlier, he mentioned a “lectotype” in the MNHN without illustration and label data (Kafanov, 1980). However, the specimen figured by him (Kafanov, 1999: pl. 2, figs. 3–6) as lectotype does not correspond with specimens stored in that museum’s type collection, although the size he gave – 62 x 54 mm – is same as of one of the specimens (MNHN 3970). It is obvious that there was confusion with the photographs and that the specimen figured by Kafanov (1999) does not belong to the type series. According to ICZN Article

74.2, if it is demonstrated that a specimen designated as a lectotype was not a syntype, it loses its lectotype status. Accordingly, we prefer to regard both MNHN specimens 3970 and 3971 as syntypes. There is no doubt that these specimens were collected by *Vénus* as the original printed label of the 19th century is present (Fig. 2C).

In the original description, Deshayes (1839) indicated the coast of California as the collecting site for this species. Kafanov (1980) restricted the type locality to Kamchatka; this species does not inhabit California and is unknown south of Ketchikan, Alaska (55.3°N) (Coan et al., 2000). Kafanov (1974) believing that *Cardium boreale* Broderip & G. B. Sowerby I, 1829, was an earlier name for this species, requested the International Commission on Zoological Nomenclature to suppress this name, but the Commission ruled that *C. boreale* is a *nomen dubium* (Melville, 1984). Coan et al. (2000) regarded *C. boreale* as a possible synonym of *Clinocardium* (*Ciliatocardium*) *ciliatum* (Fabricius, 1780), but Kafanov (1999) again placed the former species in the synonymy of *C. californiense* with a query.

Kafanov (1999) subdivided this species into three subspecies: *C. californiense californiense, C. californiense uchidai* Habe, 1955, and *C. californiense middendorffi* (Kafanov, 1999), based on the geographical variation in rib number and the valve convexity/length ratio.

It was long believed that *C. californiense* had a southern distribution limit in the northwest Pacific in the Sea of Japan side of Korea and Japan (Kafanov, 1999; Coan et al., 2000). However, there are several records of *C. californiense* from the Yellow Sea, on both the Chinese (Xu, 1964; 1997; Qi et al., 1989; Liu, 2008) and the Korean coasts (Yoo, 1976; Je et al., 1988; Kwon et al., 1993, 2001; Kwon & Lee, 1999). Xu (1964: 98) mentioned that *C. californiense* "... is found only in the deeper waters of the Yellow Sea occupied by the cold water mass ..." in a depth range of 23–77 m (Liu, 2008). We believe that part of these records refer, in fact, to *Clinocardium* (*Keenocardium*) *buelowi* (Rolle, 1896), which differs clearly from *C. californiense* in the lack of a keel twist on the posterior area of the valves and in having fewer ribs (37–38) (Kafanov, 1999). At least, illustrations in Qi et al. (1989: text fig. 141 – about 37 ribs), Yoo (1976: pl. 29: figs. 10, 11), Kwon and Lee (1999: text fig. on p. 75) might belong to *C. buelowi*. Coan et al. (2000) suggested that the relationship of *C. californiense uchidai* to *C. buelowi* has yet to be fully resolved.

Specimens collected from Yeongil Bay in Korean coast of the Sea of Japan differ from the southern subspecies *C. californiense uchidai* by the thin, interiorly colored shell with a lesser number (32–34) of sparsely spaced radial ribs, and the ratio of convexity/length is between 0.52 and 0.72 (0.59 on average) in measured specimens (Lutaenko et al., 2003). The number of ribs on specimens of *C. californiense* collected in the Okhotsk and Japan seas is between 34 and 56, but mostly about 43–51 (Lutaenko et al., 2003: fig. 4); this figure is close to that of Kafanov (1999: fig. 1) – 39–61, most often 43–53 ribs. This allows us to suggest that Korean population may belong to a distinct, as-yet unnamed species. Kafanov (2004) did not rule out this possibility.

ACKNOWLEDGMENTS

The authors are very grateful to Philippe Bouchet (MNHN), Eugene V. Coan (Palo Alto, USA), and David G. Reid (BMNH) for discussions, suggestions and assistance with literature. Bruce Marshall (The New Zealand Museum Te Papa Tongarewa, New Zealand) kindly improved the ms. Digital illustrations were prepared by K. S. Sundukov and K. A. Borzenko. This study was supported by grants from FEB RAS no. 09-I-P23-01 and no. 09-I-P15-03.

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Revised ms. accepted 26 December 2010

MALACOLOGIA, 2011, 54(1–2): 87–95

THE EFFECT OF STOCKING DENSITY ON GROWTH AND SURVIVAL OF THE FRESHWATER MUSSEL *UNIO TIGRIDIS* (BIVALVIA: UNIONOIDEA)

Hülya Şereflişan* & Erdal Yilmaz

Mustafa Kemal University, Faculty of Fisheries and Aquatic Sciences 31200,
İskenderun Hatay, Turkey

ABSTRACT

The effects of four stocking densities of 20, 40, 60, 80 mussels/m^2 on growth of *Unio tigridis* were investigated. The growth of the freshwater mussel *U. tigridis* in cages was studied for a year from March 2003 to April 2004 in Lake Gölbaşı. Juvenile mussels with the initial weight of 0.64 ± 0.08 g were stocked in metal cages placed on the lake bottom. Growth in live weight, shell length, width and height was measured monthly for the four different stock groups. Chlorophyll a, magnesium (Mg), nitrite (NO_2), nitrate (NO_3), amount of organic matters, ammonia (NH_3), phosphate (PO_4), silica (Si) and calcium (Ca) were also analyzed monthly. All water quality parameters were within proper limits for mussel culture. At the end of the study, the greatest live weight (5.55 ± 0.03 g) was obtained from 40 mussels/m^2, with 3.5 2 ± 0.02 cm and 1.47 ± 0.03 cm as length and width values, respectively. The greatest height was determined in a stocking rate of 60 mussels/m^2, with 1.99 ± 0.03 cm. Therefore, juveniles should be stocked in early spring for *U. tigridis* at a level of 40–60 individuals/m^2.

Key words: *Unio tigridis*, freshwater bivalve, mussel culture, stocking density, growth.

INTRODUCTION

Bivalve molluscs are dominant filter-feeders on most of the planktonic biomass and exert control over ecosystem structure and function (Irmgard et al., 2000). Filtration by bivalves can lead to a large decreases in phytoplankton and other particles in the water column (Welker & Walz, 1998). Freites et al. (2003) reported that growth limits in natural populations of bivalves is related to diminished food availability. Freshwater burrowing bivalves of the order Unionoida (families Unionidae, Margaritiferidae, Hyriidae, Iridinidae and Mycetopodidae) and Veneroida (families Corbiculidae and Sphaeriidae) have the potential to greatly influence freshwater ecosystem processes (Vaughn & Hakenkamp, 2001).

Freshwater mussels of the family Unionidae need to be protected because many species are threatened by extinction (Strayer et al., 2004). The global decline of freshwater mussel populations in the last five decades has caused much concern among national and international conservation organizations (Araujo & Ramos, 2000). In contrast with other unionid species, *U. tigridis* is not threatened by extinction due to environmental hazards and/or commercial use.

Unio tigridis (BOURGUIGNAT, 1852) (Unionidae) is ecologically important in southeastern Turkey (Schütt, 1983; Şereflişan, 2003, 2005, 2008). Information on the ecological importance of this species is very limited, and there have been no ecological studies of this species in Turkey. We have a few personnel communications about the ecology of *U. tigridis* in Iraq. *Unio tigridis* is benthic and lives on substrata at a depth of 1–5 m. Individuals of this species have been observed in both lakes and irrigation channels. The life cycle of unionids is remarkable and complex, with microscopic larvae of unionids (glochidia) having hooks to attach themselves to the fins or gills of host fish (Şereflişan et al., 2009). Therefore, freshwater mussels' survival depends not only on abiotic habitat conservation but also on the availability of the host fish (Araujo & Ramos, 2000; Barnhart, 2006).

Unio tigridis can grow to 8 cm long and may be considered for aquacultural purposes. Also, in souvenir markets, the nacreous layers of its shells have been used for inlays in furniture (Şereflişan, 2008). However, there have been no studies on the environmental requirements, growth and survival rates in cages in this species. Moreover, there has been no effort to culture of

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*Corresponding author: hulyasereflisan@hotmail.com

this species. Therefore, the purpose of this study was to assess the potential to culture *U. tigridis* as an alternative human food source.

Culture studies carried out on other unionids have shown differences in growth rates at different locations (Mueller & Patzner, 1996; Paterson & Nell, 1997). These differences were associated with environmental factors such as chlorophyll a, organic matter, pH and temperature (Morris & Corkum, 1999). It is now agreed that the type of aquaculture system, the stocking density, and depth should be considered among many important factors defining an aquacultural strategy for juvenile and adult stages (Taylor et al., 1998). The effects of these factors are clearly reflected by growth rate and survival (Monteforte & Morales, 2000). Additionally, temperature affects the duration of the growing season (Morris & Corkum, 1999).

To date, a great deal of research has been carried out on the biology, ecology and distribution of unionids (Strayer et al. 1994; Çek & Şereflişan, 2006). There are few publications on the culture of unionids (Lima et al., 2006), and there has been no effort to culture of *U. tigridis*. The present study was designed to determine the effect of four stocking densities on both growth and survival of this species over a 12-month period. Preliminary information about the culture of this species will be of importance for freshwater mussel aquaculturists throughout the world.

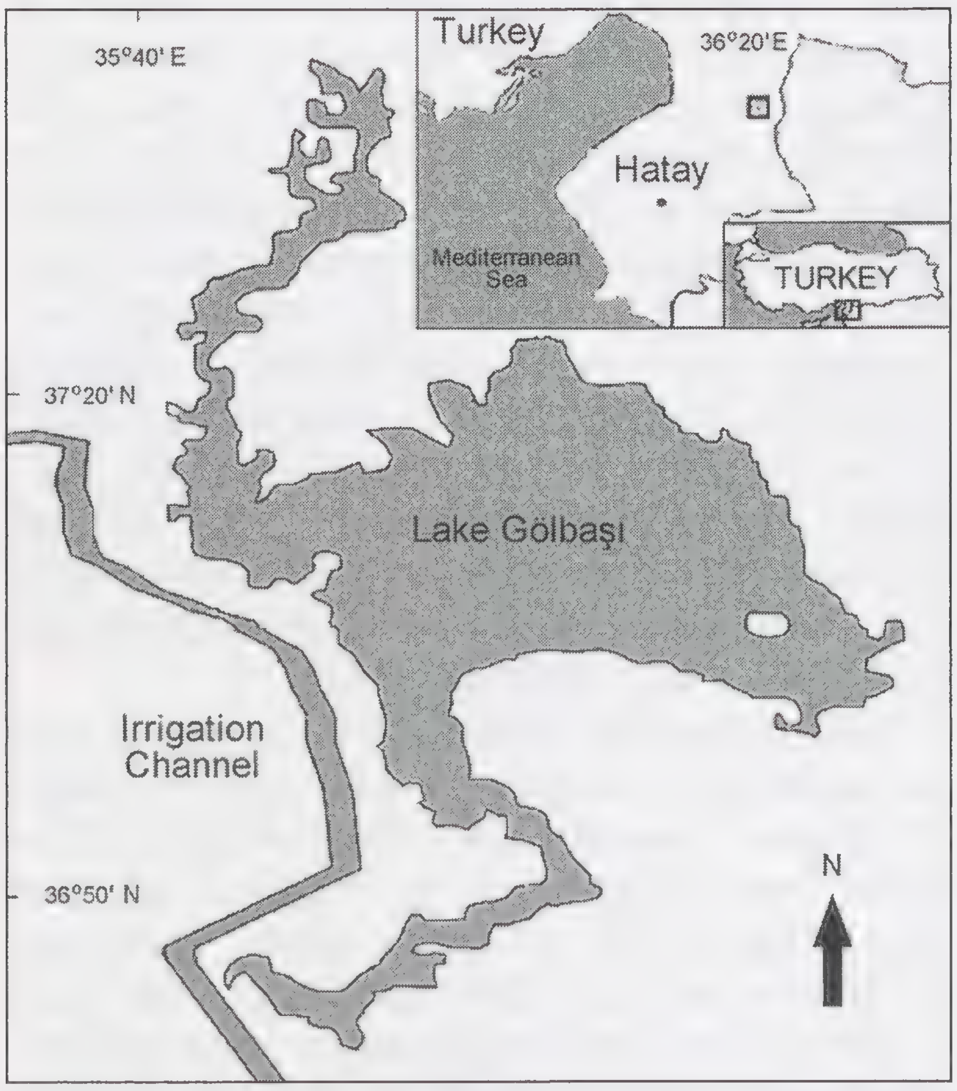

FIG. 1. Map of the study site.

MATERIAL AND METHODS

Study Site

The experiment was carried out in Lake Gölbaşı, Hatay, southern Turkey, between May 2001 and April 2002 (36°30'16"N, 36°29'42"E). Lake Gölbaşı is in the eastern Mediterranean region of Turkey, 50 km north of the city of Antakya (36°29'E, 36°30'N). The lake is a natural lake with a surface area of 12 km^2 at altitude of 80 m. The lake volume is 8,000,000 m^3, with a maximum depth of 6 m. Since it supplies water to the surrounding cotton fields, the water level is lower in spring and summer. The lake has no incoming or outgoing creeks and is only fed by spring water (Fig. 1).

Environmental Factors

Oxygen, temperature and pH were measured directly in the field with digital instruments. Oxygen and temperature were measured by YSI model 52 oxygen meter and pH by Orion model 420A pH meter. Nansen-type bottles were used for sampling for lake water. One l water samples were taken to laboratories of Mustafa Kemal University to analyze chlorophyll a (Ch a), particulate organic matter (POM), ammonia (NH_3), nitrite (NO_2), nitrate (NO_3), calcium (Ca), magnesium (Mg), phosphate (PO_4) and silica (Si). Ch a and POM samples were passed through a 150 µm nylon mesh to remove large particles. The number of particles was determined with a Fluorometrik method (APHA, 1980). The EDTA method was used to analyze calcium (Ca), magnesium (Mg), whereas a spectrophotometer was employed to analyze, ammonia (NH_3), nitrite (NO_2), nitrate (NO_3), phosphate (PO_4) and silica (Si) (APHA, 1971).

Biological Material

Juveniles were collected with a scoop net and a hand dredge at a depth of 1–3 m in Lake Gölbaşı. The initial main shell measurements were 6.2 ± 0.08 mm in length, 4.0 ± 0.01 mm in height and 2.5 ± 0.02 mm in width. The average initial weight of the juvenile mussels was 0.64 ± 0.08 g. Juveniles were stocked in cylindrical cages of one cubic m volume (115 cm diameter and 25 cm height). Cages were covered with a metal net (2 cm mesh size), and a polyamide net with 6 mm mesh size was placed on the inside of the metal net. Experimental design was four treatments with three replicates each.

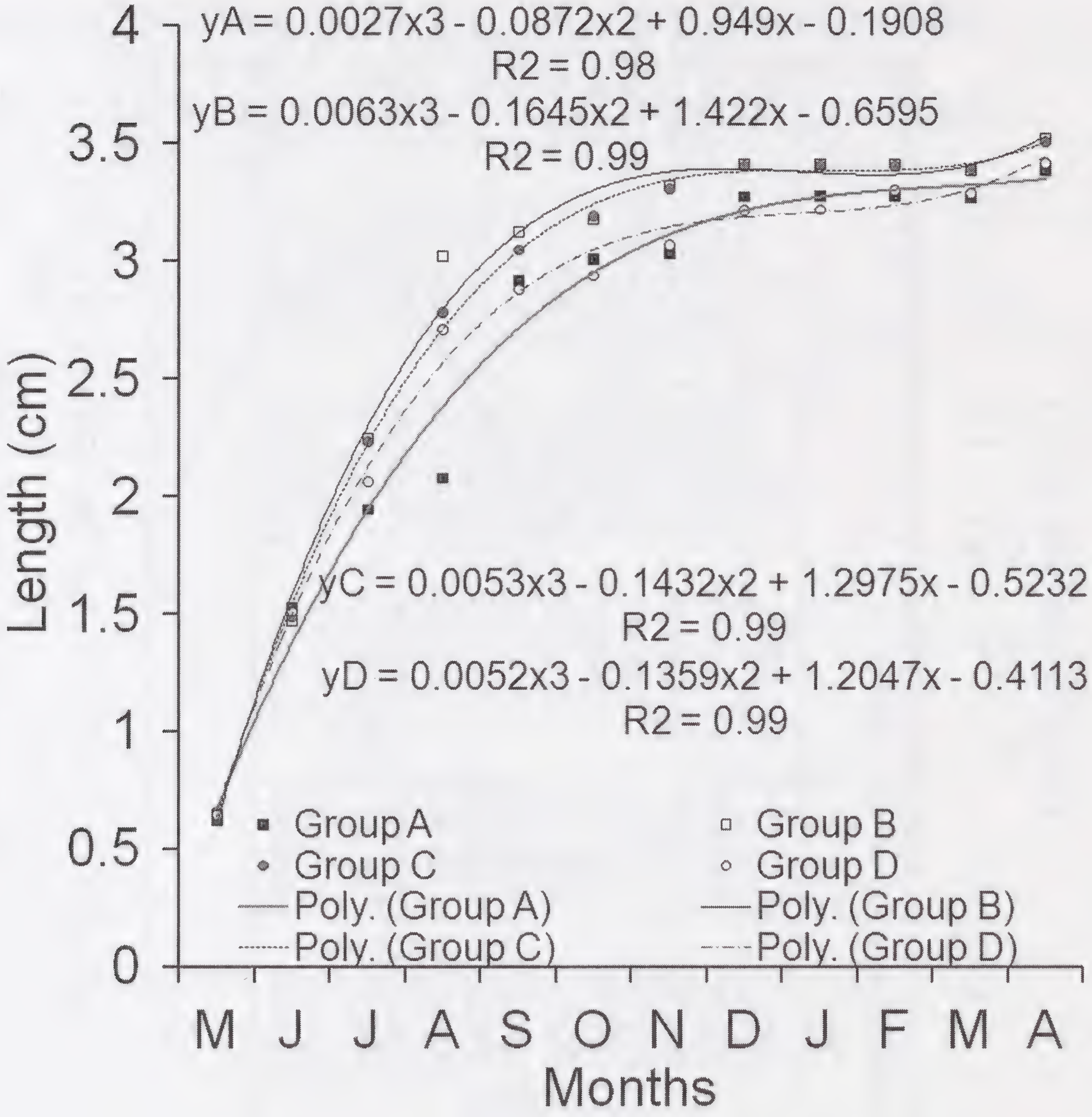

FIG. 2. Mean growth in shell length of *Unio tigridis* grown at various densities for 12 months.

Four stocking densities were used: group A with 20 mussels/m^2, group B with 40 mussels/m^2, group C with 60 mussels/m^2, and group D with 80 mussels/m^2. The juvenile mussels were placed in approximately 2 m depth in 12 metal cages.

Sampling and Biometry

Systematic sampling was conducted, and all mussel measurements were made according to Hoggarth (1999). Shell length, width, height and live weight measurements were taken monthly for 12 months, while wet meat weight measurements were determined at the end of the study. Measurements were performed by sampling of 20 mussels from each cage randomly. Mantle cavity water of the mussels sampled was drained before weighing. The growth parameters were estimated from the changes in shell length (L), live weight (LW) and wet meat weight (WMW). Mortality was determined by counting the number of empty shells in each cage monthly.

Statistical Analyses

Analysis of variance (ANOVA) was employed to detect growth differences between the stocking groups. Significance level was selected as 0.05 to measure statistical differences between treatment groups.

TABLE 1. Water quality parameters measured for a duration of 12 months in the Lake Gölbaşı of Turkey (mg l^{-1}) (mean ± SE); POM: particulate organic matter, NO_2: nitrite, NH_3: ammonia, NO_3: nitrate, PO_4: phosphate, Mg: magnesium, Si: silica, Ca: calcium.

Months	Chlorophyll a	POM	NO_2	NH_3	NO_3	PO_4	Mg	Si	Ca
May	0.83±0.01^{ef}	1.98±0.02^{de}	0.008±0.00^{a}	0.23±0.01^{c}	1.36±0.00^{c}	0.02±0.00^{a}	2.79±0.03^{ab}	4.67±0.01^{c}	4.48±0.02^{a}
June	0.78±0.01^{e}	2.03±0.04^{def}	0.009±0.00^{a}	0.39±0.01^{e}	1.40±0.01^{d}	0.02±0.00^{a}	2.76±0.05^{a}	3.06±0.00^{ab}	4.55±0.04^{ab}
July	0.36±0.02^{b}	2.45±0.01^{g}	0.017±0.00^{c}	0.28±0.01^{cd}	1.35±0.01^{c}	0.03±0.00^{b}	2.84±0.05^{bcd}	3.21±0.01^{ab}	4.55±0.04^{ab}
August	0.32±0.01^{b}	1.39±0.03^{b}	0.013±0.00^{b}	0.11±0.01^{b}	1.32±0.00^{b}	0.05±0.01^{b}	2.81±0.02^{bc}	9.47±0.01^{e}	4.45±0.03^{a}
September	0.18±0.01^{a}	2.46±0.01^{g}	0.018±0.00^{c}	0.07±0.00^{a}	1.31±0.01^{ab}	0.01±0.00^{a}	2.95±0.05^{ef}	2.98±0.01^{a}	4.56±0.03^{ab}
October	0.47±0.02^{d}	1.09±0.02^{a}	0.014±0.00^{b}	0.07±0.00^{a}	1.30±0.00^{a}	0.01±0.00^{a}	2.74±0.04^{a}	5.68±0.00^{cd}	4.46±0.02^{a}
November	0.42±0.03^{bc}	1.25±0.03^{b}	0.013±0.00^{b}	0.09±0.01^{a}	1.29±0.00^{a}	0.01±0.00^{a}	2.92±0.02^{de}	5.69±0.01^{cd}	4.56±0.05^{ab}
December	0.43±0.01^{bc}	1.53±0.02^{c}	0.009±0.00^{a}	0.08±0.01^{a}	1.29±0.00^{a}	0.01±0.00^{a}	2.93±0.02^{de}	5.48±0.00^{cd}	4.55±0.03^{ab}
January	0.48±0.02^{cd}	1.68±0.03^{cd}	0.007±0.00^{a}	0.07±0.01^{a}	1.28±0.01^{a}	0.01±0.00^{a}	2.95±0.03^{ef}	5.23±0.01^{cd}	4.53±0.02^{ab}
February	0.53±0.02^{cd}	1.78±0.01^{cde}	0.004±0.00^{a}	0.06±0.01^{a}	1.28±0.01^{a}	0.01±0.00^{a}	2.98±0.02^{ef}	5.11±0.01^{cd}	4.45±0.01^{a}
March	0.79±0.01^{e}	1.83±0.02^{cde}	0.003±0.00^{a}	0.08±0.01^{a}	1.29±0.01^{a}	0.01±0.01^{a}	2.89±0.04^{d}	5.02±0.00^{cd}	4.41±0.02^{a}
April	0.82±0.02^{ef}	1.92±0.01^{cde}	0.006±0.00^{a}	0.12±0.01^{b}	1.32±0.00^{b}	0.02±0.01^{a}	2.83±0.02^{bcd}	4.96±0.00^{c}	4.42±0.01^{a}

$^{a, b, c, d, e, f}$Letters show statistical differences in vertically ($P < 0.05$).

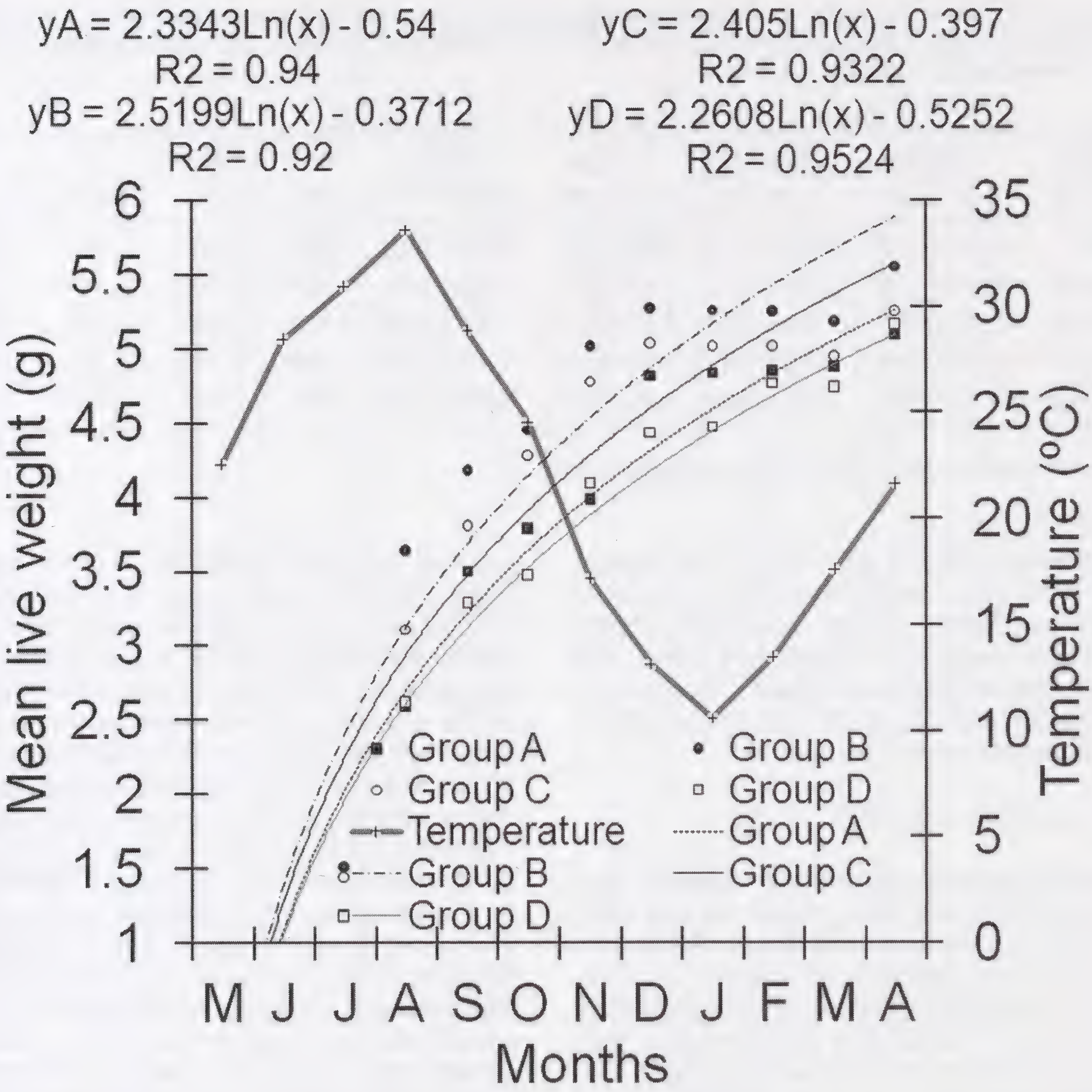

FIG. 3. Growth and temperature relationship of *Unio tigridis* grown at different densities for 12 months.

Also, growth-time regressions were calculated by estimation curves (Fig. 2). These curves are useful in estimating the appropriate data model. For this purpose, linear, logarithmic, inverse, quadratic, cubic, power, compound and exponential curves were tested to determine the best regression model. The results of variance analysis, the lowest standard error and regression coefficients were also evaluated to find best regression model. Zar (1996) was used to compare the regression equations of the models. The Excel program was used to determine the mean and standard errors for water quality parameters. All statistical analyses were carried out with the SPSS program.

RESULTS

Environmental Factors

The temperature ranged from 10.59°C in January to 33.63°C in August. Annual range of oxygen concentration was 4.51 ppm (January) to 9.60 ppm (November). The changes in pH were nearly insignificant during the course of the study. Monthly distributions of chlorophyll a (Ch a), particulate organic matter (POM), ammonia (NH_3), nitrite (NO_2), nitrate (NO_3), calcium (Ca), magnesium (Mg), phosphate (PO_4) and silica (Si) are shown in Table 1. Monthly distributions of Ch a, Ca, and Mg were

TABLE 2. The mean (x ± SD) characteristics of freshwater mussel (*Unio tigridis*) cultivated in cage and shell ratios [Group A (20 mussels/m^2), Group B (40 mussels /m^2), Group C (60 mussels/m^2), Group D (80 mussels/m^2)].

Stock Groups	Weight (W in g)	Length (L in cm)	Height (H in cm)	Width (W in cm)	W (g)/L	W (cm)/L	W (cm)/H	H/L
Initial	0.64 ± 0.08	0.62 ± 0.08	0.40 ± 0.01	0.25 ± 0.02	1.03^{a}	0.40^{ab}	0.62^{a}	0.64^{a}
Group A	5.10 ± 0.05	3.39 ± 0.02	1.88 ± 0.01	1.32 ± 0.02	1.50^{b}	0.39^{a}	0.70^{ab}	0.55^{b}
Group B	5.55 ± 0.03	3.52 ± 0.02	1.96 ± 0.02	1.47 ± 0.03	1.57^{c}	0.42^{b}	0.75^{b}	0.55^{b}
Group C	5.24 ± 0.05	3.50 ± 0.03	1.99 ± 0.03	1.47 ± 0.02	1.49^{b}	0.42^{b}	0.73^{b}	0.56^{b}
Group D	5.16 ± 0.04	3.42 ± 0.03	1.89 ± 0.01	1.35 ± 0.04	1.50^{b}	0.39^{a}	0.71^{ab}	0.55^{b}

$^{a, b, c}$Letters show statistical differences in vertically ($P < 0.05$).

significantly different ($P < 0.05$). The highest Ch a (0.83 ± 0.01 mg/L) and NO_3 (1.40 ± 0.01) levels were in May, and the highest NH_3 (0.39 ± 0.01) level was in June. POM (2.46 ± 0.01) and NO_2 (0.018 ± 0.00) were highest in September, and the highest PO_4 (0.05 ± 0.01) and S (9.47 ± 0.01) levels were in August.

Shell and Tissue Growth

Mean characteristics of these mussels, such as weight (W), length (L), height (H) and width (W) are summarized in Table 2. All groups showed fast growth from May to October. Length increment differed significantly among the groups ($P < 0.05$). The growth in length was determined to be the highest in group C (60 mussels/m^2) (Fig. 2). It was determined that both stocking density and water temperature affected mussel growth (Fig. 3). Wet meat weight was highest in the stocking group B of 40 mussels/m^2, and wet meat yields of 20 mussels/m^2 and 40 mussels/m^2 were found to be higher than that of the stocking groups of 60 and 80 mussels/m^2 (Fig. 4a). A negative growth rate was observed in winter months, followed by a quick recovery in spring. Positive significant relationships were found between width-length and width-height ratios for all groups ($P < 0.05$).

DISCUSSION

Older reports, such as Coker et al. (1921), and more recent research on unionids (Beaty & Neves, 1996; Hoggarth 1999; Morris & Corkum, 1999) are essential to have an understanding of the main growth characteristics of freshwater mussels. In culture conditions, stocking density is an important factor causing growth differences in live weight, wet meat weight and shell growth (Sereflisan, 2003). It was determined that stocking densities had a significant effect on the shell length, wet meat weight and live weight growth of *U. tigridis* for the duration of 12 months ($P < 0.05$). Considering all growth characteristics, the best growth was achieved in group B (40 mussels/m^2). Growth characteristics of mussels were expected to be higher for the lower stocking densities compared to the higher densities due to less competition (Mackie, 1984). Our results, however, indicated that there was not an inverse relation between growth and stocking density. This mode of growth pattern may be related to such behavioral characteristics as proper site selection and food search, and protection against predators. Also, Mackie (1984) reported colonial living and higher growth for the freshwater mussels at a particular stocking density and supported our findings. There has been no study focused on the effect of stocking density on survival of *U. tigridis*. In our study, it was determined that stocking densities had no effect on survival rate. In an earlier study, survival rates of the Asian freshwater mussel *Limnoperna fortunei* stocked at the different rates were not significant and showed high survivorship for all groups (95%) at the end of the trial (Boltovskoy & Cataldo, 1999).

The greatest growth of shell length was determined to be in spring and summer months in group C (60 mussels/m^2). However, it was determined that shell length growth of *U. tigridis* was better in warmer months than that in the cold months for all stocking groups. The Asian freshwater mussel *Limnoperna fortunei*

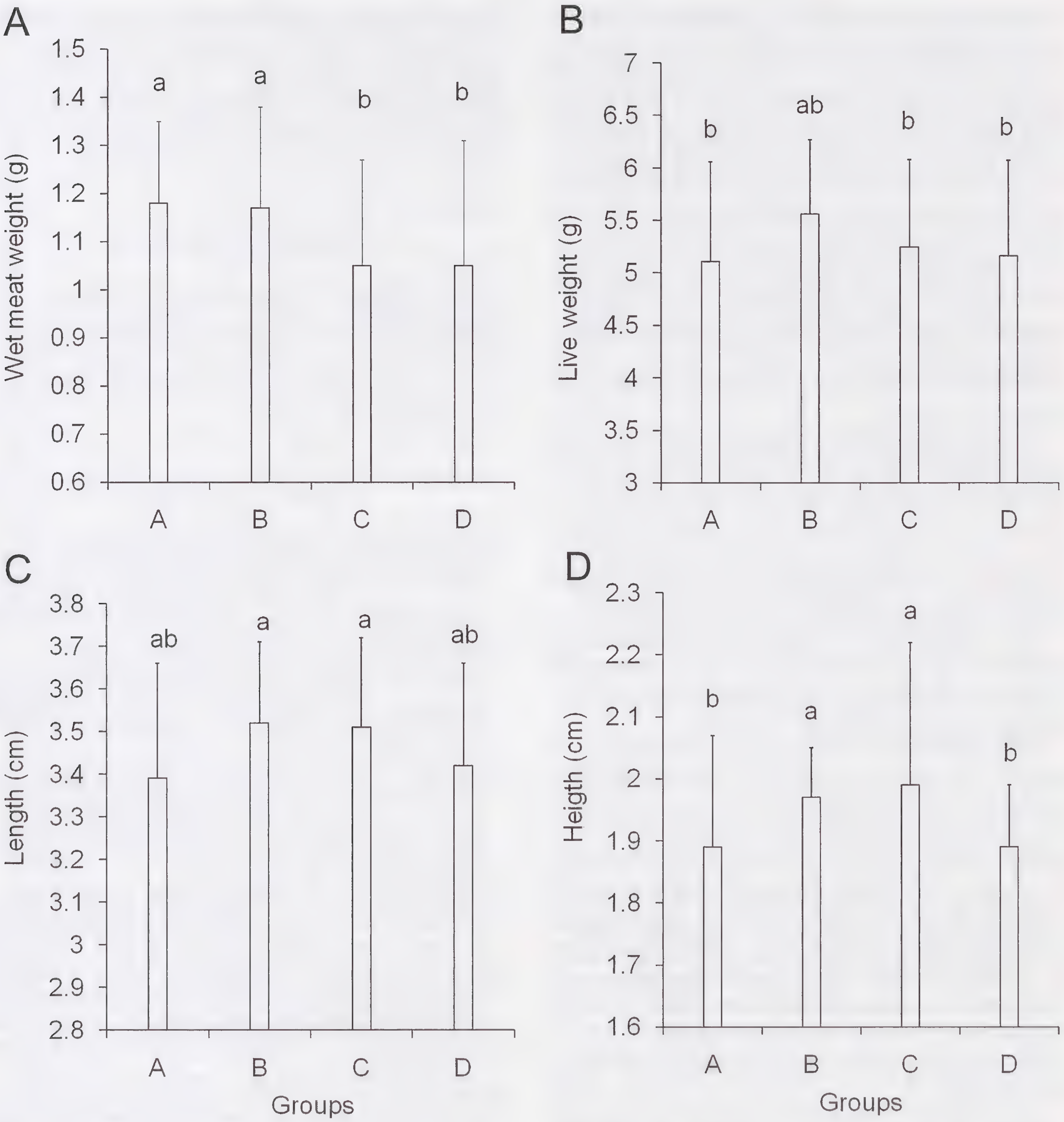

FIG. 4. Growth of each group of *Unio tigridis* as wet meat weight (A), live weight (B), length (C) and height (D) grown at different densities for 12 months.

also grew better in warm than in cold months (Boltovskoy & Cataldo, 1999) at different stocking densities. Also, Mallet et al. (1987) indicated that the rate of shell length and wet meat weight increases in mussels are greater in warm regions than in cold regions.

Oxygen and pH values are as important as temperature and have a profound effect on all living organisms (Morris & Corkum, 1999; Karayücel & Karayücel, 2000b). In our study, pH and oxygen values were changed by temperature. Unionids are able to live at a pH of 4.7 (the minimum level) and to reproduce and grow at pH values between 5.6–8.3 (McMahon, 1991). pH levels of our study are within the range of 7.78 ± 0.04 – 8.02 ± 0.01, which is in accordance with the literature. The fertility of natural waters generally increases with the increase in total hardness (Tepe & Boyd, 2003; Tepe, 2009). Hard waters often have moderate to high total alkalinities, are well buffered at a neutral to slightly alkaline pH, and tend to be more productive than poorly mineralized, acidic waters (Boyd & Tucker, 1998). Nitrate-nitrogen (NO_3-N) level (1.01–1.43 mg/L) was within the optimum range for living biomass in our study. The low nitrite-nitrogen (NO_2-N) value in our study indicated that the lake water has enough oxygen for nitrification. Organic matter concentration in lake water varied between 1.23–3.22 mg/L. This variation might be due to precipitation and runoff. The highest silica value in the lake was 9.47 ± 0.01 in August. The silica level can be low during spring when algae population is the highest, and this level may also show differences depending on season, water flow and precipitation.

Despite the fact that mussel growth is strongly related to annual primary productivity, it is not as related with chlorophyll a concentration (Small & Van Stralen, 1990). In shallow lakes, increased phytoplankton and zooplankton levels do not mean that the season has a direct effect on the chlorophyll a level (Adrian et al., 1999). Our findings, confirming to the literature, showed that the mussel growth levels were the highest in August, and the chlorophyll a levels were the highest in April and May.

Transparency, viscosity and hardness of lakes and rivers can change due to springs or other incoming waters, but there was no incoming water source in our study area. Low growth even atrophy can be seen in mussels in waters with a low calcium concentrations (McMahon, 1991). Calcium is vital for mussel shell deposition (McMahon, 1991). Mallet et al. (1987) reported that the accumulation of calcium in mussel shells during the juvenile stage is very rapid, and shell growth in contrast to meat growth does not depend on food availability.

Other factors influencing mussel growth are water depth and bottom structure, which can impact the growth of the unionid *Anodonta cygnea* (Mueller & Patzner, 1996). The growth decreases in deeper water, and mussels placed in the baskets cultivated in sediment grew better than those on rocky or other hard substrata (Paterson & Nell, 1997). The present study was performed on the sediment at a depth of 1.5–2.0 m, and these conditions were optimum for the culture of this species.

The present study gives preliminary information on the effect of stocking density on growth of *U. tigridis* cultured in cages for 12 months. Also, we examined the some water quality criteria influencing primary productivity of the lake. Since highest live weight and shell height were obtained from the stocking groups of 40 mussels/m^2 and 60 mussels/m^2 in spring and summer, it is advisable to stock juveniles in early spring for *U. tigridis* at a level of 40–60 individuals/m^2. Other unionids should be similarly evaluated in future investigations.

ACKNOWLEDGEMENTS

I am grateful to Menderes Şereflişan for scuba diving and collecting samples, and to Yalçın Tepe for assisting with English. Metin Kumlu made useful suggestions that improved the manuscript.

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Revised ms. accepted 3 December 2010

MALACOLOGIA, 2011, 54(1–2): 97–108

TAXONOMIC STUDY OF SHALLOW-WATER OCTOPUSES (CEPHALOPODA: OCTOPODIDAE) IN JAPAN AND ADJACENT WATERS USING MITOCHONDRIAL GENES WITH PERSPECTIVES ON OCTOPUS DNA BARCODING

Natsumi Kaneko[1, 2], Tsunemi Kubodera[1*] & Akira Iguchi[3]

ABSTRACT

A recent study revised the generic level taxonomy of the family Octopodidae, and several species groups that were previously included in *Octopus* are now recognized as independent genera. However, knowledge regarding phylogenetic relationships among taxa in the family Octopodidae is still poor. The phylogenetic relationships of shallow-water benthic octopus species in Japan and adjacent waters were examined in the present study using mitochondrial DNA cytochrome *c* oxidase subunits I and III (COI and COIII, respectively) sequence data, and the taxonomic statuses of the octopus species were compared to those derived by morphological identification. We obtained COI (657 bp) and COIII (464 bp) sequences from 45 taxa assigned to 34 species of seven genera. Samples used were voucher specimens stored in the National Museum of Nature and Science, Tokyo. Sequences of the genes of both *Haliphron atlanticus* and *Tremoctopus violaceus* from GenBank were included as outgroup taxa. Additionally, sequences of the genes of *Octopus vulgaris* obtained from Mediterranean coast of France, which is type locality of this species, was also included from GenBank in order to discuss about status of Japanese *O. vulgaris*. Through phylogenetic analyses, we recognized *Callistoctopus* and a distinct group including four *Octopus* species and an *Enteroctopus* species, which was designated the "*Enteroctopus* group" in the present study, with high bootstrap support. *Amphioctopus* was not completely distinguished because it sometimes formed a clade together with *Hapalochlaena*, which shows morphological affinities with *Amphioctopus*. *Abdopus* + *O. laqueus* + *O. cyanea* and *O. vulgaris* + *O. oliveri* were recognized as distinct groups, but the phylogenetic support for these groups was weak. For identifying species using short DNA sequences, sequence divergences were calculated using COI sequences. Sequences within and among species were generally divergent enough to discriminate the species, but several overlaps with intra- and interspecific divergence caused by poor taxonomic resolution were also observed. Although performing species identification using DNA sequences from shallow-water benthic octopus species is premature, the results in this study indicated the possible application of COI sequences in octopus species identification, thereby providing a preliminary dataset for future DNA barcoding of octopus.

Key words: phylogenetic relationships, shallow-water benthic octopus species, mitochondrial genes, species identification, DNA barcoding.

INTRODUCTION

Octopus is a cosmopolitan genus and has been a source of taxonomic confusion with respect to the family Octopodidae. A recent study demonstrated that the generic-level taxonomy of the family Octopodidae needs major revision, and that several species groups that were previously included in *Octopus* are now recognizable as independent genera (Norman & Hochberg, 2005). Several new or resurrected genera were presented based on those species groups, and the generic statuses of several species were changed. However, phylogenetic support for these newly independent genera is still poor, and *Octopus* still remains a heterogeneous assemblage as has been demonstrated in recent years through several studies.

Several studies have been conducted to determine phylogenetic relationships among octopus species based on molecular analysis. The non-monophyletic status of *Octopus* was

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[1] Department of Zoology, National Museum of Nature and Science, 3-23-1 Hyakunin-cho, Shinjukuku, Tokyo 169-0073, Japan
[2] Okinawa Enetech Co., Inc., 5-2-1 Makiminato, Urasoe, Okinawa 901-2131, Japan
[3] Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus, 3422 Sesoko, Motobu, Okinawa 905-0227, Japan
*Corresponding author: kubodera@kahaku.go.jp

demonstrated in previous studies based on molecular analysis using mitochondrial genes (Carlini et al., 2001; Takumiya et al., 2005). Moreover, molecular analysis data obtained using two mitochondrial DNA genes, cytochrome *c* oxidase subunit III (CO III) and cytochrome b (CYTB), and a nuclear DNA elongation factor gene indicated the non-monophyletic status of *Octopus* and established several monophyletic groups, which might represent independent genera (Guzik et al., 2005), thereby supporting recent taxonomic changes. However, knowledge regarding phylogenetic relationships among taxa in the family Octopodidae is still restricted to a few species, and further accumulation of molecular data, especially data associated with morphological information, is required.

Here we examined the molecular phylogeny of shallow-water benthic octopus species distributed in Japan and adjacent waters, which include the northern part of the Indo-West Pacific region. Previous studies on the taxonomy of shallow-water benthic octopus species distributed in Japan and adjacent waters have recognized more than 80 species (Sasaki, 1929; Taki, 1942, 1963, 1964; Okutani et al., 1987). Recent studies have revised these previous works, added several new species, and discovered high species diversity within the benthic octopus species in this area (Kubodera & Lu, 2002; Kaneko & Kubodera, 2005; 2007a, b). We analyzed phylogenetic relationships among these diverse octopus taxa using DNA sequence data obtained from mitochondrial cytochrome *c* oxidase subunit I (COI) and COIII genes. Our analysis compared the classification of DNA data obtained from museum-stored materials with their historical classification based on morphology. We studied the phylogenetic relationships of shallow-water benthic octopus species collected from Japan, Taiwan, and Vietnam, and compared the taxonomic statuses of these species with those derived from morphological identification. The results of this study will also provide a provisional dataset for future DNA barcoding of octopus, which was introduced for the Class Cephalopoda at the Cephalopod International Advisory Council in 2006 (Strugnell & Lindgren, 2007).

MATERIALS AND METHODS

Specimens and DNA Tissue Samples

Specimens examined in this study were collected during surveys conducted from 1998 to 2007 in Japan, Taiwan, and Vietnam (Kubodera & Yamada, 1998; Kubodera, 2001; Kubodera & Yamada, 2001; Kaneko, 2006; Kaneko et al., 2008). Specimens were identified to the lowest possible taxon based on morphological characteristics. Small tissue samples were taken from the mantles or arms of the specimens and stored in 99% ethanol for DNA extraction. The specimens were subsequently fixed in 10% formalin and later stored in 40% isopropanol. All specimens and tissue samples were registered and deposited in the National Museum of Nature and Science, Tokyo (NSMT), Japan.

Selection of Specimens for Analysis

From the NSMT collection, 45 specimens were selected, and their taxonomical statuses were identified morphologically. We used “cf.” for provisionally identified species, and the attribution of genus was generally according to a previous study (Norman & Hochberg, 2005).

Polymerase Chain Reaction Amplification and Sequencing

DNA was extracted using a phenol/chloroform extraction protocol. A partial segment of mitochondrial COI was amplified using primers LCO1490 and HCO2198 (Folmer et al., 1994). The primers used for mitochondrial COIII were Ooc3F and Ooc3R (Guzik et al., 2005).

Polymerase chain reaction (PCR) was performed in volumes of 50 µL containing 0.2 mM of each dNTP, 1.5 mM $MgCl_2$, 0.4 µM of each primer, and 1.0 unit of Taq DNA polymerase (Takara Ex Taq™; Takara Bio Inc., Otsu, Japan). Amplifications for COI were performed using a Takara PCR Thermal Cycler MP (Takara) under the following conditions: 30 s at 94°C, 30 s at 45°C, and 60 s at 72°C (35 cycles). The samples were incubated at 94°C for 3 min before the cyclic reactions and at 72°C for 5 min after completion. Amplifications for mitochondrial COIII were performed under the following conditions: 30 s at 94°C, 30 s at 50°C, and 60 s at 72°C (40 cycles) with the final extension step performed at 72°C for 5 min.

We placed 5 µL of the reaction product on a 1.5% agarose gel in 0.5X Tris/Borate/EDTA (TBE) buffer to check the success of the reaction. The remaining PCR product was purified using ExoSAP-IT (Amersham Biosciences, Piscataway, New Jersey, USA).

PCR products were sequenced using the BigDye Terminator Cycle Sequencing v3.1 Cycle

Sequencing Kit (Applied Biosystems, Foster City, California, USA) on an ABI PRISM™ 3100-Avant (Applied Biosystems). Sequencing reactions were performed in volumes of 20 µL containing 3.0 µL of Terminator Ready Reaction Mix, 2.5 µL of 5X sequencing buffer, and 3.2 pmol of the appropriate sequencing primer. The reactions were performed under the following conditions using the Takara PCR Thermal Cycler MP (Takara): 30 s at 96°C, 15 s at 50°C, and 4 min at 60°C (25 cycles). Samples were incubated at 96°C for 1 min before the cyclic reactions. Products were purified using ethanol/EDTA/sodium acetate precipitation according to the sequencing kit manual. Sequencing for COIII samples was performed by Macrogen Inc. (Seoul, South Korea). Sequences were aligned using ATGC ver. 4.0.10 and Genetix ver. 7.0.8 (Genetix Ltd., New Milton, UK).

Data Analysis

We performed maximum parsimony (MP) and maximum likelihood (ML) analyses to construct the phylogenetic trees. MP analyses for COI and COIII datasets were performed separately using PAUP*4.0b10 (Swofford, 2002). In addition, we performed a combined analysis of COI and COIII data because the incongruence length difference test (ILD test; Farris et al., 1994), which was performed using PAUP*4.0b10 (Swofford, 2002; 1,000 replicates of heuristic searches), suggested no significant phylogenetic difference between the two datasets (P = 0.783). MP analysis was performed using heuristic searches with 100 random addition analyses and TBR branch swapping. Robustness of each phylogenetic tree was tested by bootstrapping (1,000 replicates).

Prior to performing ML analysis, we searched the best-fit model of evolution using ModelTest (Posada & Crandall, 1998), and the GTR+I+G model (Rodriguez et al., 1990) was selected as the best-fitting model for COI (invariable sites: 0.5755, gamma distribution parameter: 1.1120), COIII (invariable sites: 0.4655, gamma distribution parameter: 0.7436), and combined datasets (invariable sites: 0.5226, gamma distribution parameter: 0.8136). ML analyses were performed using PhyML (Guindon & Gascuel, 2003; Guindon et al., 2005). Robustness of each phylogenetic tree was tested by bootstrapping (100 replicates) with nearest-neighbor interchange branch swapping. Sequences of the genes of both *Haliphron atlanticus* and *Tremoctopus violaceus* from GenBank were included as outgroup taxa (accession numbers: AF377964, AF377978, GU288525 and GU288522). Additionally, sequences of the genes of *Octopus vulgaris* obtained from Mediterranean coast of France (Allcock et al., 2006), which is type locality of this species, was added to the datasets from GenBank (accession numbers: EF016328, EF016319). *Octopus vulgaris* is a type species of genus *Octopus*, which is a core problem of the recent generic confusion of Octopodidae.

RESULTS

Morphological Taxonomy

The selected 45 specimens were identified as 34 species and were assigned to the following seven genera: *Abdopus*, *Amphioctopus*, *Callistoctopus*, *Cistopus*, *Enteroctopus*, *Hapalochlaena*, and *Octopus*. Specimen data listed in Table 1 included species name, NSMT registered number, collection date and site, and site number as shown in Figure 1, and GenBank accession numbers.

The study also included *Callistoctopus minor*, the taxonomic status of which has been assigned as *Octopus* or as unclear (Toll & Voss, 1998; Norman & Hochberg, 2005). However, we placed this species in *Callistoctopus* because we considered that its morphological characteristics, such as long arms with the dorsal pair being the longest, moderate to high gill lamellae counts (10–14 per demibranch), and a large copulatory organ on the right arm 3 are diagnostic of the genus (Robson, 1929; Taki, 1942, 1964; Voss, 1981; Norman, 1992a). This species has been morphologically classified into the following three subspecies: *O. minor typicus*, *O. minor pardalis*, and *O. minor minor* (Sasaki, 1929; Toll & Voss, 1998). Here we classified the specimen as *O. minor typicus*.

Although *O. megalops* was considered to be a synonym of *O. hongkongensis* (Gleadall, 1993), we found a specimen in our collection having characteristics similar to those of *O. hongkongensis*, but the specimen had an extremely large eye, which is a notable characteristic of *O. megalops* (Taki, 1964). Here we classified this specimen as *O.* cf. *megalops* and included it in the dataset of molecular analysis.

Three unidentified species (*Callistoctopus* sp. 1–3) (Kaneko et al., 2008) were also included in the dataset.

TABLE 1. List of specimens used for analysis in this study. Abbreviations indicate the areas of sample collection (EC, East China Sea; JP, Japan; OG, Ogasawara Islands; RK, Ryukyu Islands; TW, Taiwan; and VN, Vietnam), and site numbers are associated with the numbers in Fig. 1.

Species	Museum No. (NSMT-Mo.)	Collection Date	Collection sites	Site No.	Gen. Bank Acc. No.	
					COI	COIII
Amphioctopus marginatus	74708	00/06/04	East China Sea	EC	AB430521	AB573195
Amphioctopus marginatus	74816	02/01/14	Nha Trang, Vietnam	VN2	AB385870	AB573196
Amphioctopus marginatus	74597	01/10/19	Uraga, Tokyo Bay, Japan	JP4	AB430522	AB573194
Amphioctopus cf. *neglectus*	74819	02/01/14	Nha Trang, Vietnam	VN2	AB385872	AB573190
Amphioctopus cf. *rex*	75217	03/12/06	Nha Trang, Vietnam	VN2	AB385871	AB573191
Amphioctopus cf. *siamensis*	76109	07/05/26	Wuchi market, Taiwan	TW	AB430516	AB573192
Amphioctopus aegina	76110	07/05/26	Wuchi market, Taiwan	TW	AB430515	AB573189
Amphioctopus kagoshimensis	76116	03/02/01	Jogashima Is., Japan	JP4	AB430520	AB573193
Amphioctopus ovulum	72114	00/05/10	Tosa Bay, Japan	JP6	AB430524	AB573197
Amphioctopus ovulum	74751	00/06/04	East China Sea	EC	AB430523	AB573198
Amphioctopus cf. *ovulum*	74820	02/01/19	Nha Trang, Vietnam	VN2	AB385873	AB573199
Amphioctopus fangsiao	74749	00/06/24	East China Sea	EC	AB430518	AB573186
Amphioctopus fangsiao	71636	99/11/09	Seto Inland Sea, Japan	JP5	AB430519	AB573187
Amphioctopus fangsiao	76107	07/05/26	Wuchi market, Taiwan	TW	AB430517	AB573188
Hapalochlaena fasciata	76117	02/10/05	Tateyama, Chiba, Japan	JP3	AB430529	AB573212
Hapalochlaena lunulata	76017	06/11/20	Miyagi Is. Okinawa, Japan	RK1	AB430530	AB573213
Hapalochlaena maculosa	76111	07/05/26	Wuchi market, Taiwan	TW	AB430531	AB573214
Abdopus aculeatus	75974	03/11/24	Iriomote Is. Okinawa, Japan	RK2	AB430514	AB573185
Abdopus abaculus	76100	07/10/28	Ikei Is. Okinawa, Japan	RK1	AB430513	AB573184
Cistopus cf. *indicus*	74822	02/09/22	Cat Ba, Vietnam	VN1	AB385878	AB573210
Octopus vulgaris	71640	99/10/19	Seto Inland Sea, Japan	JP5	AB430546	AB573217
Octopus vulgaris	74600	00/06/18	Misaki, Sagami Bay, Japan	JP4	AB430547	AB573219
Octopus vulgaris	74775	00/06/19	East China Sea	EC	AB430548	AB573218
Octopus parvus	76119	04/02/20	Misaki, Sagami Bay, Japan	JP4	AB430544	AB573216

(continues)

(continued)

	Museum No.	Collection			Gen. Bank Acc. No.	
Species	(NSMT-Mo.)	Date	Collection sites	Site No.	COI	COIII
Octopus cyanea	75911	95/02	Ogasawara Is., Japan	OG	AB430534	AB573223
Octopus cyanea	75995	06/11/30	Nakagusuku, Okinawa, Japan	RK1	AB430535	AB573224
Octopus oliveri	75913	95/02	Ogasawara Is., Japan	OG	AB430532	AB573226
Octopus laqueus	75992	06/11/08	Miyagi Is. Okinawa, Japan	RK1	AB430543	AB573215
Octopus incella	76101	07/11/07	Motobu, Okinawa, Japan	RK1	AB430542	AB573225
Octopus wolfi	76113	07/08/15	Kadena, Okinawa, Japan	RK1	AB430545	AB573227
Octopus megalops	72110	99/11/16	Tosa Bay, Japan	JP6	AB430538	AB573220
Octopus conispadiceus	75134	01/09/15	Off Kushiro, Hokkaido, Japan	JP2	AB430533	AB573222
Octopus longispadiceus	72212	00/10/20	Seto Inland Sea, Japan	JP5	AB430539	AB573228
Octopus hongkongensis	76118	03/03	Misaki, Sagami Bay, Japan	JP4	AB430537	AB573221
Enteroctopus dofleini	76115	03/	Wakkanai, Hokkaido, Japan	JP1	AB430536	AB573211
Callistoctopus luteus	76114	07/11/10	Ohdo, Okinawa, Japan	RK1	AB430526	AB573208
Callistoctopus luteus	74595	00/12/10	Miura, Sagami Bay, Japan	JP4	AB430527	AB573206
Callistoctopus luteus	74814	02/01/14	Nha Trang, Vietnam	VN2	AB385874	AB573207
Callistoctopus aspilosomatis	75986	06/11/08	Miyagi Is. Okinawa, Japan	RK1	AB430525	AB573205
Callistoctopus sp. 1	75219	03/12/06	Nha Trang, Vietnam	VN2	AB385875	AB573203
Callistoctopus sp. 2	75221	03/12/06	Nha Trang, Vietnam	VN2	AB385876	AB573204
Callistoctopus sp. 3	74815	02/01/19	Nha Trang, Vietnam	VN2	AB385877	AB573202
Callistoctopus ornatus	75982	06/11/21	Ohdo, Okinawa, Japan	RK1	AB430528	AB573209
Callistoctopus minor typicus	74731	00/06/18	East China Sea	EC	AB430540	AB573201
Callistoctopus minor typicus	71634	99/11/16	Seto Inland Sea, Japan	JP5	AB430541	AB573200

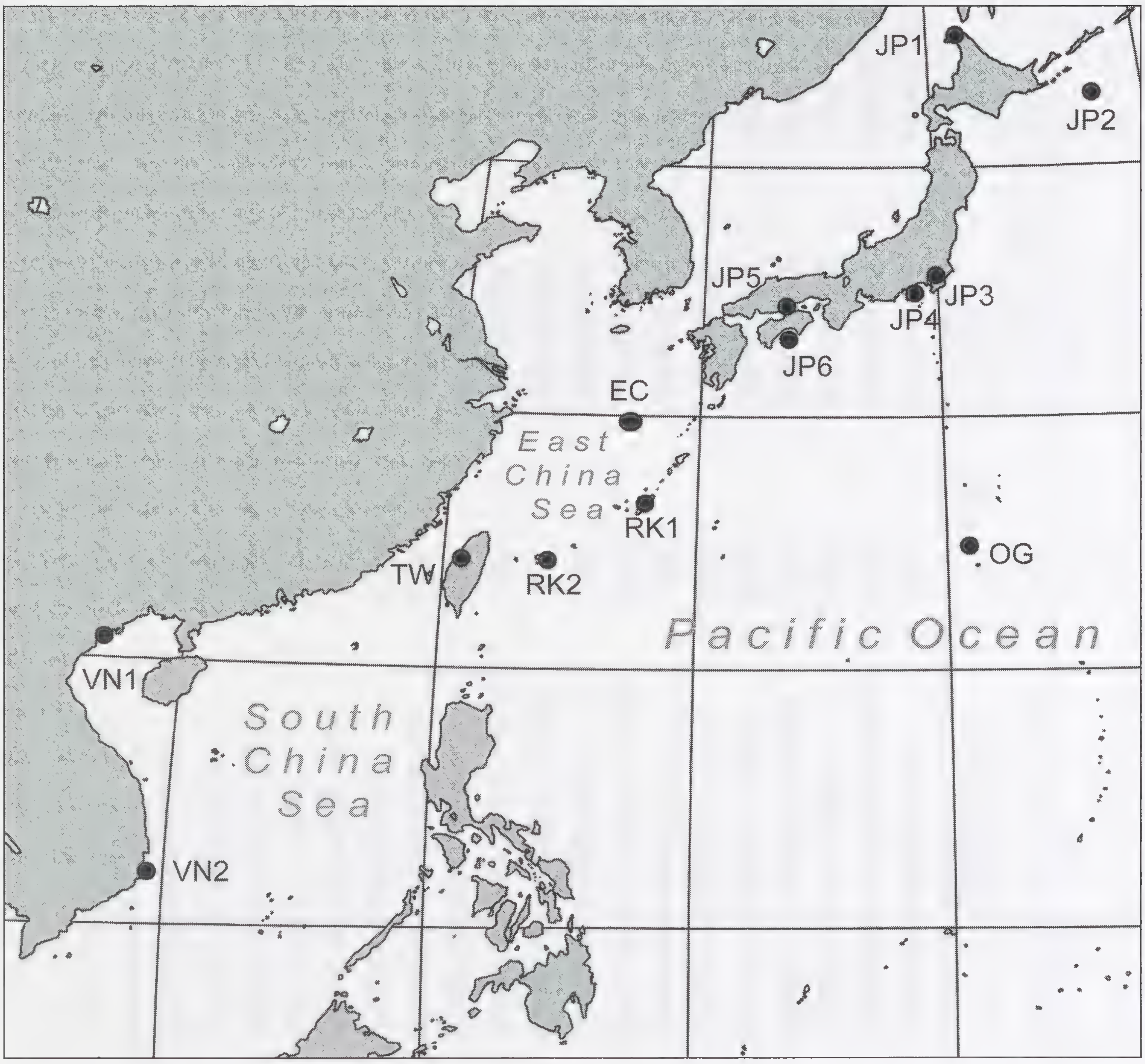

FIG. 1. Specimen collection sites. Abbreviations indicate the areas of sample collection (EC, East China Sea; JP, Japan; OG, Ogasawara Islands; RK, Ryukyu Islands; TW, Taiwan; and VN, Vietnam).

Phylogenetic Analyses

We obtained a total of 1,121 bp from mitochondrial COI (657 bp) and COIII (464 bp) sequences.

The combined ML analysis tree (Fig. 2) supported monophyly of both *Callistoctopus* and *Hapalochlaena*, with a high bootstrap value (100%). A clade including *Enteroctopus dofleini* and 4 *Octopus* species was also supported by a bootstrap value of 100%. In this study, we refer to this clade as the "*Enteroctopus* group." *Amphioctopus* appeared to be monophyletic, but support for monophyly was not high (79%). The two *Abdopus* species were sister taxa with 83% bootstrap support; however, the *Abdopus* + *O. laqueus* + *O. cyanea* clade was supported by a high bootstrap value (94%).

The combined MP analysis tree (Fig. 3) also supported monophyly of *Callistoctopus* and the "*Enteroctopus* group" with high support (> 99%). However, monophyly of *Amphioctopus* was not supported; this genus formed a supported clade together with *Hapalochlaena*. There was low support (74%) for *Abdopus*. In comparison with the ML tree, the MP tree did not find significant support for the *Abdopus* + *O. laqueus* + *O. cyanea* clade (58%).

Both ML and MP trees recovered the *O. vulgaris* + *O. oliveri* clade, but its support was relatively low (≤ 77%) in both topologies. *Octopus vulgaris* from the Mediterranean Sea was included in this clade.

Intra- and Interspecies Sequence Divergence

Seven species of three genera, including 18 specimens, were sampled from multiple localities (Table 1). Sequence divergence in the COI sequence, which was obtained from the same

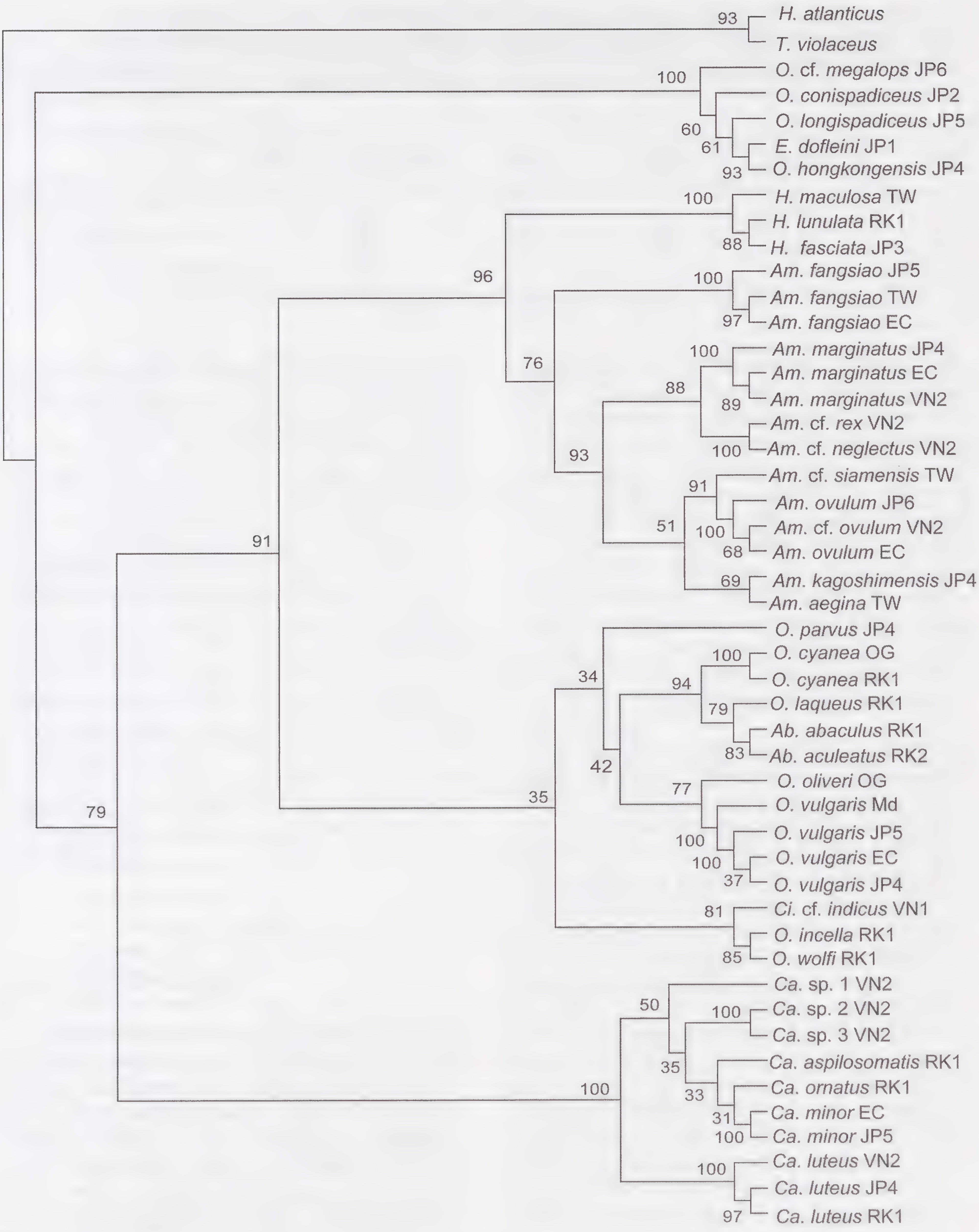

FIG. 2. Phylogram for shallow-water benthic octopus species distributed in Japan and adjacent waters including *Octopus vulgaris* from Mediterranean Sea and for outgroup taxa (*Haliphron atlanticus* and *Tremoctopus violaceus*) based on the maximum likelihood analysis of combined mitochondrial COI and COIII sequences (GTR+G+I model). Numbers beside branches are bootstrap percentages. Abbreviations after the species name indicate the collection site as shown in FIG. 1 (EC, East China Sea; JP, Japan; Md, Mediterranean Sea; OG, Ogasawara Islands; RK, Ryukyu Islands; TW, Taiwan; and VN, Vietnam).

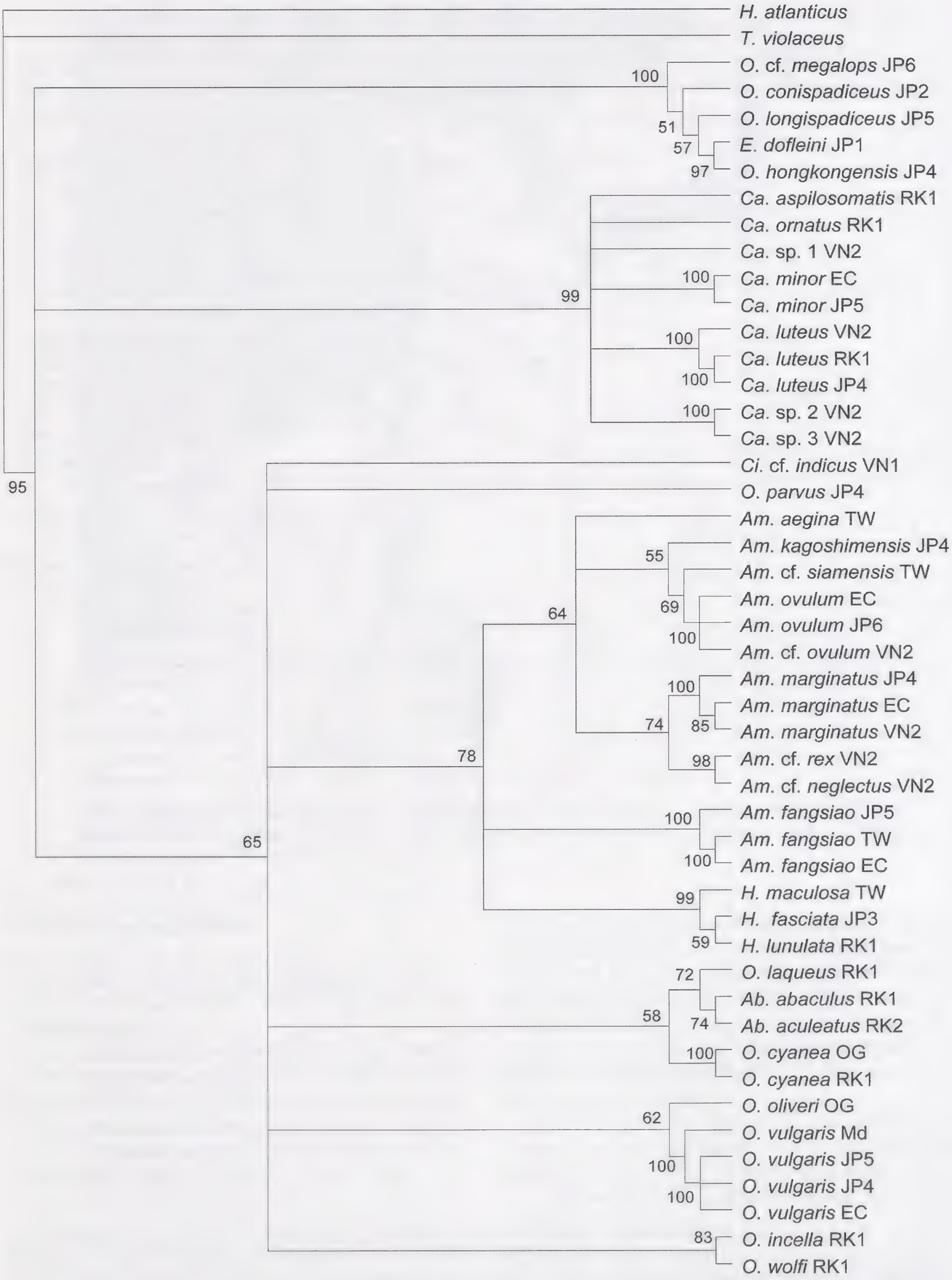

FIG. 3. Phylogram for shallow-water benthic octopus species distributed in Japan and adjacent waters including *Octopus vulgaris* from Mediterranean Sea and for outgroup taxa (*Haliphron atlanticus* and *Tremoctopus violaceus*) based on the maximum parsimony analysis of combined mitochondrial COI and COIII sequences. Numbers beside branches are bootstrap percentages. Abbreviations after the species name indicate the collection site as shown in FIG. 1 (EC, East China Sea; JP, Japan; Md, Mediterranean Sea; OG, Ogasawara Islands; RK, Ryukyu Islands; TW, Taiwan; and VN, Vietnam).

TABLE 2. COI sequence variation within and between sibling species of shallow water benthic octopuses. Pairwise genetic distances were calculated by PAUP* (Swofford, 2002) using the GTR + G + I model of nucleotide evolution. The minimum, max, mean and standard deviation were calculated for pairwise comparisons within species and between sibling species.

	No. of combinations	Min	Max	Mean	SD
Intraspecific	20	0.00	0.07	0.02	0.02
Interspecific (between sibling species)	45	0.04	0.51	0.28	0.11

species from different localities and calculated using the GTR + G + I model, ranged from 0.00 to 0.07, with an overall average of 0.02. On the other hand, divergence among sibling species, which was also calculated using the GTR + G + I model, ranged from 0.04 to 0.51, with an overall average of 0.28 (Table 2). No differences (0.00) were observed between *Am. marginatus* specimens collected from the East China Sea and Vietnam, and *O. vulgaris* specimens collected from the East China Sea and Japan stations 5 and 6. Divergence between Japanese and the Mediterranean *O. vulgaris* was 0.02. The highest intraspecies divergence (0.07) was observed in *Am. fangsiao* specimens collected from Japan station 5, East China Sea, and Taiwan. The lowest interspecies divergence (0.04) was observed in *Ca.* sp. 2 and *Ca.* sp. 3 specimens collected from Vietnam.

DISCUSSION

Taxonomic Implications

Our phylogenetic analyses of shallow-water benthic octopus species distributed in Japan, Taiwan, and Vietnam, using partial mitochondrial gene sequences, recovered clades in support of two less well-understood genera.

A *Callistoctopus* clade received high bootstrap support in both analyses. This genus, previously referred to as the "*Octopus macropus* species group" (Guzik et al., 2005), was not monophyletic in this prior study, falling in a clade with *Grimpella*. Comparing our results with this previous study is difficult because the targeted DNA regions and species in the two studies are quite different. However, our conclusion here is that *Callistoctopus* is a distinct genus, as suggested by Norman & Hochberg (2005).

Monophyly of the "*Enteroctopus* group" in the present study was clearly supported with a high bootstrap value. Of the species therein, only "*dofleini*" has been previously correctly placed in *Enteroctopus*. *Octopus hongkongensis* and *O. conspadiceus* were previously placed in *Paroctopus* (Robson, 1929). However, Norman & Hochberg (2005) included only *P. digueti* in this genus and excluded several species endemic to the North Pacific Ocean. The generic statuses of *megalops* and *longispadiceus* have not yet been determined; currently, they are placed in *Octopus* (Taki, 1964; Takeda, 2003). Our results suggest they should be placed in *Enteroctopus*.

The statuses of *Amphioctopus* and *Hapalochlaena* were equivocal. A *Hapalochlaena* clade was supported by a high bootstrap value in the combined ML tree, but it formed a clade together with *Amphioctopus* in the MP tree. *Hapalochlaena* species are known as blue-ringed octopus and are easily recognized by the dramatic appearance of iridescent blue rings or lines on the dorsal body surface, which distinguishes *Hapalochlaena* as a distinct genus. However, *Hapalochlaena* and *Amphioctopus* share some diagnostic characteristics, such as presence of short arms (2–3× mantle length) and ocelli on the arm base. In addition, *Hapalochlaena* species and *Am. mototi*, a small ocellate *Amphioctopus* species distributed in the Indo-West Pacific, are known to possess strong venom in their salivary gland (Sheumack et al., 1978; Norman, 1992b, 2000). These evidences of morphological affinities and our results of molecular analysis indicate close evolutionary relationships between these two genera.

The affinities of species previously assigned to *Octopus* are still not well understood. We believe that the clade including specimens identified as *O. vulgaris* and *O. oliveri* might truly belong to *Octopus*, because *O. vulgaris* from the Mediterranean Sea, the type species of this genus from the type locality, was included in this clade. Although a number of regional populations of octopus species, which are designated *O. vulgaris*, have been observed and identification of many of these populations needs reexamination, the Japanese population of *O. vulgaris* and Mediterranean population seem to be conspecific in accordance with the low value of sequence divergence among them (0.02). The Mediterranean sample represents genuine *O. vulgaris*, and consequently our result supported the identification of Japanese population.

Abdopus was considered to be a distinct genus, but its bootstrap values were divergent in different topologies (ML tree: 83%; MP tree: 74%). It forms a clade with *O. laqueus* and *O. cyanea* consistently, both of which are distributed in coral reef areas. The topology indicated that the *Abdopus* species and *O. laqueus* showed a close relationship with each other, even though *O. laqueus* never perform arm autotomy, a characteristic behavior of *Abdopus* species. Huffard (2007) reported an *Abdopus* species, *Ab. undulates*, possessing similar morphological characteristics to those of *O. laqueus* collected from Tonga, indicating a close similarity between these taxa. A close relationship was observed between *Abdopus* species and *O. cyanea* (Guzik et al., 2005). This evidence indicates an evolutionary relationship of these species in coral reef areas, regardless of morphological variety. The generic statuses of *O. cyanea* and *O. laqueus*, along with those of a number of recognized and unrecognized coral reef species, await further studies.

Cistopus is characterized by the presence of water pouches on the oral surface of the webs between the arms, and males have a tiny conical ligula without a calamus. This genus inhabits muddy bottom areas of the South China Sea. In the ML tree, *Cistopus* cf. *indicus* formed a clade with *O. incella* and *O. wolfi*, which are pygmy species without water pouches that inhabit clear water coral reef areas. No morphological or ecological affinities were observed among these species, and further investigation is required to resolve their taxonomic status.

Species Identification using COI Region

The use of short DNA sequences for species identification has recently attracted great attention under the term DNA barcoding. The method promises to assign an unknown sample to a known species and to support explorative studies to discover potentially undescribed species. It may also enable the large-scale identification of organisms in ecological or genomic studies (Blaxter, 2004). The sequence divergence at mitochondrial COI regularly enables the discrimination of closely allied species in all animal phyla except Cnidaria (Hebert et al., 2003). Availability of DNA barcoding using COI sequences for cephalopods were demonstrated by Allcock et al. (2011) in their study on deep sea octopus, *Pareledone*. Our study found that the mean value of intraspecific variation at COI in benthic octopus species was much lower than the mean value of interspecific divergence (intraspecific: 0.02; interspecific: 0.28), also indicating that mitochondrial COI would be the appropriate region to discriminate species of the benthic octopus.

However, the accuracy of barcoding for species identification depends on the extent of, and the separation between, intraspecific variation and interspecific divergence in the selected markers. The overlap of genetic variation within species and divergence among sibling species makes barcoding less effective (Meyer & Paulay, 2005). In our result, overlap of intraspecific variation with interspecific divergence also existed. We identified three specimens from different localities as *Am. fangsiao*, but sequence variation among individuals of *Am. fangsiao* was 0.07, which was greater than the minimum value for interspecific divergence (0.04). *Am. fangsiao* is a taxonomically complicated species and is at times referred to as “Iidako.” Some different morphological types have been reported within this species. Two different varieties or subspecies in *Am. fangsiao*, i.e., *Am. fangsiao* var. *typicus* and *Am. fangsiao* var. *echuanus* have been recognized in a previous study (Sasaki, 1929). The diagnostic character of these two types determined by Sasaki is a brick-colored patch on head between eyes, dumbbell or elliptical in shape in var. *typicus*, and crescent shaped in var. *echuanus*. None of our specimens possessed the crescent patch between the eyes. One of the analyzed specimens showed a dumbbell-shaped patch, and the others showed an elliptical patch. The result indicated the presence of cryptic species in *Am. fangsiao*, but at present, this species is treated as a single species comprising a number of synonyms (Gleadall & Naggs, 1991; Norman & Hochberg, 2005). Comprehensive revision of this species together with resolution of associated nomenclatural problems is required. Not only in the case of *Am. fangsiao*, but a number of taxa in Octopoda face the same problem. Several names of these taxa that can cause misunderstanding should be reorganized in accordance with zoological nomenclature standards for identification by both genetic and morphological methods.

Studies on the effectiveness of DNA barcoding on taxonomically well-understood taxa demonstrated that DNA barcoding is much less effective for identification in taxa where taxonomic scrutiny has not been thorough, and species recognition is limited to a few traditional data sets, untested by additional studies and tools (Meyer & Paulay, 2005). The shallow-water benthic octopus is currently one such group, and further accumulation of DNA datasets associated with taxonomically well-examined voucher specimens as well as comprehensive taxonomic and phylogenetic frameworks is required for effective identification through DNA barcoding.

ACKNOWLEDGMENTS

We thank Ms. T. Ogo and Dr. I. Nishiumi for technical advice and help; Dr. C. C. Lu and Ms. C. W. Ho for their kind assistance in sample collection in Taiwan; Dr. F. G. Hochberg for his kind review of a draft of this paper. We also appreciate Dr. A. L. Allcock and two anonymous reviewers for their valuable comments. This study was based on the following two research projects of the National Museum of Nature and Science: “Synthetic Studies on Natural History of Japanese Archipelago” and “Collection Building and Natural History Studies in Asia and the Pacific Rim” and was partially supported by the Grant-in-Aids for International Scientific Research (Field Research) of the Ministry of Education, Culture, Sports, Science and Technology of Japan (No. 08041161) and International Scientific Research of Japan Society for the Promotion of Science Fellows (No. 13575014).

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Revised ms. accepted 15 January 2011

MALACOLOGIA, 2011, 54(1–2): 109–118

GENDER-BASED DIFFERENCES IN FLORIDA APPLE SNAIL (*POMACEA PALUDOSA*) MOVEMENTS

Patricia L. Valentine-Darby[1], Philip C. Darby[2*] & H. Franklin Percival[3]

ABSTRACT

Gastropod movements have been studied in the context of habitat selection, finding food and mates, and avoiding predation. Many of these studies were conducted in the laboratory, where constraints on spatial scale influence behavior. We conducted a field study of Florida apple snail (*Pomacea paludosa*) movements using telemetry. We hypothesized that Florida apple snail movements were driven by reproductive activity, and that gender differences would be evident. We documented male and female directions and distances traveled. We also conducted a trapping study that included conspecific bait to test if the presence of females attracted more males as measured by M:F ratios in traps. The greatest distances traveled were by males, and males were more likely to maintain a consistent bearing compared to females. Male distances peaked in what typically corresponds to peak breeding season. M:F ratios in traps were positively associated with reproductive activity in the study population as measured by egg cluster counts. Conspecific bait had no effect on the number of males or females captured. However, if a female crawled into the trap, we observed greater numbers of males compared to those with no trapped females. Males may have tracked females to increase mating encounters, following slime trails, as seen in other aquatic (including other *Pomacea*) snails. The capacity for mate finding has implications for reproductive success in the relatively low density populations often seen for *Pomacea paludosa*.

Key words: *Pomacea paludosa*, reproduction, movements, Florida, apple snail.

INTRODUCTION

A gastropod's capacity for movement directly affects its ability to find suitable habitat in heterogeneous environments (Coffin et al., 2008), food (Snider & Gilliam, 2008), and mates (Erlandsson & Kostylev, 1995), and to avoid predation (Dickey & McCarthy, 2007) (also reviewed by Croll, 1983). Although many environmental factors affect the direction and distance traveled by snails (e.g., currents and benthic habitat structure, as described in Hoffman et al., 2006), chemoreception appears to be the principle mode by which many snail species' movements are directed (Croll, 1983). Snails may respond to chemicals in the trails of other snails, or to air-borne (for terrestrial snails) or water-borne chemical gradients of food, predators, or other snails (Dinter, 1974; Takeda & Tsuruoka, 1979; Croll, 1983; Shaheen et al., 2005). Much of the research on aquatic snail movements reflects laboratory studies at relatively small spatial scales, compared to the natural environments across which snails traverse. The Florida apple snail (*Pomacea paludosa* Say) (Gastropoda: Ampullariidae) is the largest native freshwater snail in North America (Pennack, 2001), with a range restricted primarily to the lakes and wetlands of peninsular Florida (Thompson, 1984). Darby et al. (2002) reported average weekly distances traveled by Florida apple snails as 15 m/wk. This led to questions about what drives apple snail movements under natural conditions. Apple snails did not move along gradients of temperature, dissolved oxygen, or water depth (to avoid being stranded in a drying marsh) during a March–June field study in Florida (Darby et al., 2002). Apple snails did move among a wide range of habitat types, including sawgrass (*Cladium jamaicense* Crantz), cattail (*Typha* spp.), and wet prairie (dominated by low profile grasses and sedges), as indicated

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[1] The Pomacea Project, 1765 East Nine Mile Road, Suite 1, #369, Pensacola, Florida 32514, U.S.A.
[2] Department of Biology, University of West Florida, 11000 University Parkway, Pensacola, Florida 32514, U.S.A.
[3] Florida Cooperative Fish and Wildlife Research Unit, U.S. Geological Survey, University of Florida, Gainesville, Florida 32611, U.S.A.
*Corresponding author: pdarby@uwf.edu

by telemetry and mark-recapture studies (Darby et al., 2002; Valentine-Darby et al., 2008). Peak apple snail egg cluster production most often occurs in April–May (Darby et al., 2008), so movement patterns during this time of year may be associated with reproduction. In lieu of environmental factors being the primary driver of the magnitude and direction of snail movements, at least during spring and summer, we hypothesized that Florida apple snail movements vary as a function of gender and changes in their reproductive status as seen in other aquatic snails (Pardo & Johnson, 2004).

Apple snails are dioecious (Aldridge, 1983). Females must find suitable structure for above-water egg cluster deposition (i.e., oviposition), typically emergent plant stems with diameters > 6 mm (Turner, 1996). Florida apple snails often occur at densities < 0.2 snails/m^2 (Darby et al., 2006), so their ability to track down potential mates may be especially critical for recruitment in many central and south Florida wetlands. Hanning (1979, p. 45) stated that "Females are searched for by the males ..."; he referred to both laboratory and field observations, but provided no information on how he came to this conclusion. A recent laboratory study of *Pomacea canaliculata* found that both males and females followed mucous trails of snails of the opposite sex (Takeichi et al., 2007); males were also attracted to water conditioned with females, suggesting an attraction to one or more water-borne sex pheromones.

We used a combination of telemetry and trapping studies to examine whether variation in distance and movement patterns of Florida apple snails in the field was associated with gender and/or reproductive activity. We hypothesized that snail movement rates were positively associated with reproductive activity (as indicated by egg cluster counts). We also hypothesized that males and females would exhibit different patterns of movement over space and time, in part because of earlier suggestions that males track down females (as noted above), and because females must target microhabitat patches that support oviposition.

METHODS

Study Area and Sampling Periods

Our study site was in the eastern-most portion of the Blue Cypress Water Management Area (BCWMA), part of the Upper St. Johns River Basin, in Indian River County, Florida. Details of the study site, including a map, were published in Darby et al. (2002). The plant community in this area consisted of a mosaic of sawgrass patches surrounded by emergent macrophytes (primarily *Eleocharis cellulosa* and *Panicum hemitomon*) and scattered areas of open water (Lowe, 1983; Darby et al., 2002). The telemetry study was conducted March–July, 1995, and the wire funnel trap study was conducted February–August, 1996. Both studies included the seasonal initiation, April–May peak, and subsequent decline of snail egg production, as described in Darby et al. (2008). We studied the same BCWMA snails in 1995 that were the subject of Darby et al. (2002) and Darby et al. (2003). We used an airboat to access the study site, but all visual searches, tracking of snail movements, and trap checks were conducted on foot.

Telemetry Study

We used miniature radio-transmitters (1.6 gram) to track snail movements. Details on transmitter attachment and monitoring were described in Darby et al. (2002). Adult apple snails (n = 47) were collected using visual searches and wire funnel traps. Visual searches consisted of collecting female snails nearing their completion of egg-laying at night, and from daytime searches for snails in clear water. Twenty-four snails were sexed based on shell morphology (Hanning, 1979), seven females were identified while laying eggs, and 16 snails were found mating (in some cases with a snail already bearing a transmitter). Copulating pairs were gently pulled apart; males were identified by their penis sheath (Hanning, 1979; also see Andrews (1964), and Albrecht et al. (1996) for observations of *P. canaliculata*). We noted that egg-laying females and mating males had the characteristic shell morphology by which we identified gender for the aforementioned 24 snails.

Hanning (1979) estimated that sexual maturity for *P. paludosa* was ≥ 30 mm shell length, so snails exceeding this length were assumed to be sexually active in our study. We placed transmitters on 25 females (shell lengths 36 to 53 mm) and on 22 males (36 to 46 mm). The transmitters were attached to the outside of the snail shell using the minimum amount of marine epoxy required for a firm hold. Snails with transmitters were returned to their original location within 20 minutes of capture. Snails were released throughout the study period in a staggered entry design to replace dead snails or transmitters with dead batteries (details in Darby et al., 2002).

We used standard telemetry equipment to locate radio-bearing snails within a 2 to 3 m diameter circle. Magnet-induced signal alteration (Darby, 1999) was used to pinpoint each snail location. On every monitoring occasion, each snail was picked up to confirm that it was alive and then returned to its exact location. Snail locations were marked with polyvinylchloride (PVC) poles driven into the substrate, and we wrote the radio-frequency of each snail on its PVC marker.

Distances traveled ($n = 81$) were documented at weekly intervals until the snail or the transmitter battery died. Movements starting from initial capture locations were excluded from analyses, because of the disturbance caused by snail handling and transmitter attachment. We also excluded locations of snails found dead. Each time a snail was located, the straight-line distance between its current location and its last-monitored location was recorded. A compass was used to measure the direction the snail had moved from its previous location. Other metrics measured at each location during the telemetry study (e.g., temperature, dissolved oxygen, depth) have been reported in Darby et al. (2002).

Telemetry Data Analyses

We have already reported the effects of environmental metrics (depth, temperature, oxygen) on the movements of the 47 snails with transmitters discussed herein, and no significant trends were found (Darby et al., 2002). Water temperatures during the study, all measured between 11:30 and 13:00 hrs, averaged (± SD) 28.8 ± 3.3°C. When temperatures fall below approximately 20–21°C, apple snail movements decline significantly (Stevens et al., 2002), but temperatures never fell below 23°C in our radio-telemetry study. Only snail movements in water ≥ 10 cm deep were included in our analyses, because in shallower depths snails stop moving (Darby et al., 2002).

We used a mixed model ANOVA (snails monitored = random effect; gender and week monitored = fixed effects) for all analyses of snail distances traveled. The analysis produces F-statistics that are not a ratio of sums of squares, but are instead from a Wald-test (Searle et al., 1992). Distances traveled (m) were transformed using the function $\log_{10}(m + 1)$ in order to meet assumptions of ANOVA.

We tested for the effects of gender, biweekly interval (e.g., March 1–14; March 15–28), and their interaction, on the weekly distances traveled. We grouped weekly data into biweekly intervals (BWI) to increase our sample size; due to deaths and battery failure, we often had ≤ 2 individuals to monitor in a given week. We increased our sample size to 4–6 (the number of different individuals for which we documented movements) by analyzing data as a function of BWI. If an individual snail's movements were measured twice within a BWI, the mean value for the 7-d distances traveled was used for that individual for that BWI. We performed repeated measures ANOVA (Crowder & Hand, 1990; SAS, 1992) to account for repeated measure of individual transmitter-bearing snails over two or more BWIs. We further explored the gender*BWI interaction using the SLICE procedure in SAS; that is, we partitioned the interaction effect to distinguish between variation in female versus male movements over time (SAS, 1992).

We constructed patterns of movement (distances and directions) for snails ($n = 11$) that were monitored on three or more occasions. We used Watson's two-sample test (U^2) (Jammalamadaka & Sengupta, 2001) to analyze the turning angles (i.e., the angle created by the intersection of two consecutive movement vectors) to see if the two sets of angular data (male and female) had the same distributions. Critical values for the test statistic and associated P-values for small sample sizes were obtained from Mardia (1972). We also tested if there was a gender difference for maintaining a bearing (degrees from north) over several consecutive movements using a Raleigh test (R) (Jammalamadaka & Sengupta, 2001). The specific direction to test for each snail was determined by the compass direction created by the line that intersected the start and end point from a series of movements.

Trapping Study

Wire funnel traps are a form of passive trapping that requires snails to move into the traps. We used a modified version of a commercially available crayfish trap; for details, see Darby et al. (2001). Pilot studies of funnel trap protocols led us to two important points regarding the use of these traps. First, bait was not needed to attract snails to the traps (Darby et al., 2001); snails entered the traps during horizontal movements and/or vertical ascents to breathe air. Second, sex ratios of captured snails suggested that males may have followed females into the traps; whenever we found a female, one to six males were also in the trap.

We hypothesized that as reproductive activity increased (as measured by egg production; see below), the male to female ratio (M:F) of captured snails in the traps would increase. Hurdle (1974) and Hanning (1979) observed that individual females mate frequently, with multiple males, throughout the egg-laying season. Andrews (1964) described multiple males attempting to mate with individual *Pomacea* females. Females lay egg cluster masses at an average rate of approximately one cluster each one to two weeks (at times producing up to three a week) for up to several months (Hurdle, 1974; Hanning, 1979). Therefore, egg laying activity should track mating activity, and increased male efforts to find mates should result in increased M:F ratios in traps. Our hypothesis regarding increased M:F ratios was based in part on Hanning's (1979) report of males tracking females. Hanning also reported a breeding season (January–June) sex ratio of 1:1 for *P. paludosa* in Florida (Lake Okeechobee), with an overall ratio, based on 868 snails collected over 1.5 years of monthly samples, of 1 female to 0.75 males. Population sex ratios of approximately 1:1 have been reported in other *Pomacea* species (Yusa & Suzuki, 2002; Cowie, 2002). Consequently, deviation from a 1:1 ratio in passive traps reflects differences in male versus female capture rates. [Funnel traps do not randomly sample the population as indicated by highly skewed M:F ratios observed in our pilot study. Randomly sampling our study population to obtain the population sex ratio, for example, via throw traps, required considerable time and labor (Darby et al.,1999) beyond the scope of our resources at the time.]

We also tested whether or not baiting traps with live apple snails attracted snails, presumably via a water-borne pheromone. To hold the bait, we constructed an 8 cm-diameter cylindrical enclosure to set inside the funnel trap and permit the bait (snail) to reach the surface to breathe air. A cylindrical bait enclosure was installed in all traps. Approximately one-third of the traps were baited with adult females (F), one-third of the traps with adult males (M), and the remaining traps were not baited and served as controls (O). Traps were numbered, and the same type of bait was used in a given trap throughout the study.

We conducted six one-week trapping sessions from January 30–August 19. We initiated a trap session by placing 51 to 54 traps on PVC poles, approximately 5 m apart, throughout our study site. At the initiation of each of the six trapping sessions, traps were randomly distributed among the PVC poles to avoid any potential effect of trap location. Traps were placed in 20 to 60 cm of water from 1 to 10 m away from the ecotone created by sawgrass and mixed-emergent wet prairie habitats.

Traps were checked twice, at 3- to 4-day intervals, during each trapping session. Traps were not moved between checks. We measured the water temperature between 11:00 and 13:30 at each trap check. [The difference between surface temperatures and those near the substrate were consistently < 1°C apart, so we based our analyses on just surface temperatures.] During each trap check, the shells of at least 20 males and 20 females (randomly selected) were measured to ensure M:F ratios were based on adult-sized snails. Captured snails were released approximately 2 m from the trap.

Egg cluster production was monitored and used as an index of reproductive activity over time (e.g., Hanning, 1979; Darby et al., 2008). We sampled three transects during each session. A transect was a 30 m length of the outer edge of a sawgrass patch bordering our study sites, that is, we sampled the sawgrass-prairie ecotone (see Darby et al., 1999). Since we were primarily interested in the temporal pattern of egg cluster production, we sampled the same three transects, starting at the same point and moving in the same direction, at each monthly count. We deployed a 1 x 2.5 m PVC quadrat 12 times along each transect during each count.

Trap Data Analyses

We examined the effect of bait type (M, F or 0) using two separate analyses. First, we looked only at the number of males captured as a function of bait type (males= bait + session + session*bait). In the second, we looked at the number of females captured (females= bait + session + session*bait). The number of snails captured per trap (male or female) in each trap session was the total of both trap checks within each 7-d trapping session. Male or female snail counts were analyzed using a generalized linear models approach based on a Poisson distribution. The goodness-of-fit criterion indicated overdispersion, so we corrected for this using the pscale option in SAS (1992) based

TABLE 1. Results of mixed model ANOVA for snail distances traveled over the seven-day interval as related to biweekly interval (BWI), gender, and their interaction, and results of partitioning the gender*BWI effect (to distinguish between BWI effects for male and female 7-d distances) using the SLICE procedure in SAS (details in Methods).

Source	Numerator DF	Denominator DF	F Value	P-Value
GENDER	1	27	0.01	0.939
BWI	8	22	2.53	0.041
GENDER*BWI	7	22	2.10	0.086
female	8	22	1.39	0.257
male	7	22	3.64	0.009

on McCullagh & Nelder (1989). Male to female ratios were calculated for each trapping session. We excluded all trap checks with no snails and all traps that had no females (M:F for an individual trap would be undefined). [The effect of bait was ignored, see Results.] We tested the hypothesis that M:F ratios were positively correlated with egg cluster counts during the same period using Spearman's rank correlation analysis, and we report the average ratio and SE for each trap session based on ratios from individual traps. The sample size varied from 27 to 36 M:F ratios for each trap session. We also used the same approach to test the competing hypotheses that M:F ratio was associated with the linear progression of time (as trap session 1 through 6, representing February through August) or water temperature.

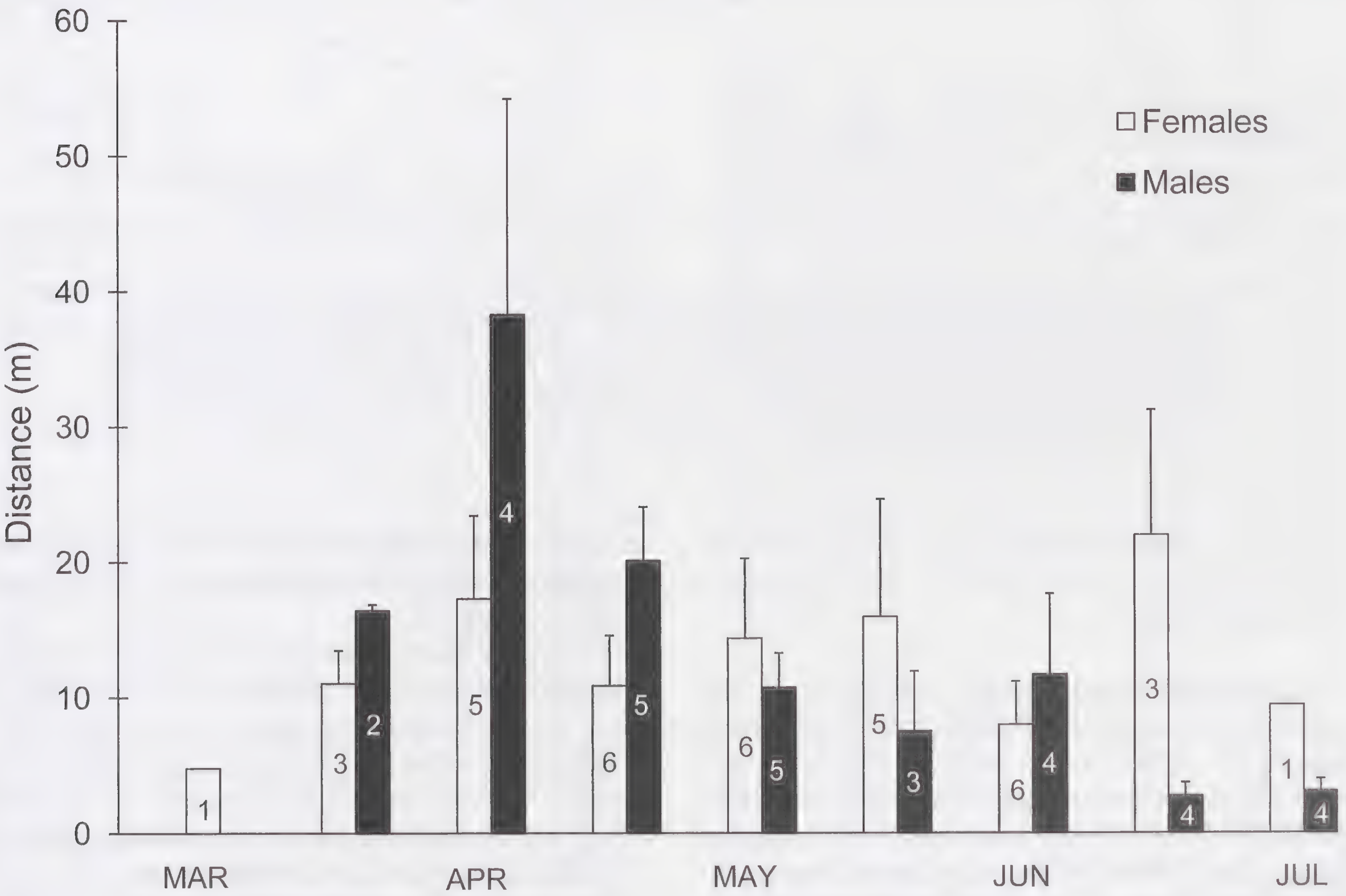

FIG. 1. Weekly distances traveled by male and female snails in BCWMA in 1995. Data are from snails in water depths > 10 cm. Error bars are standard errors. Sample sizes appear inside bars.

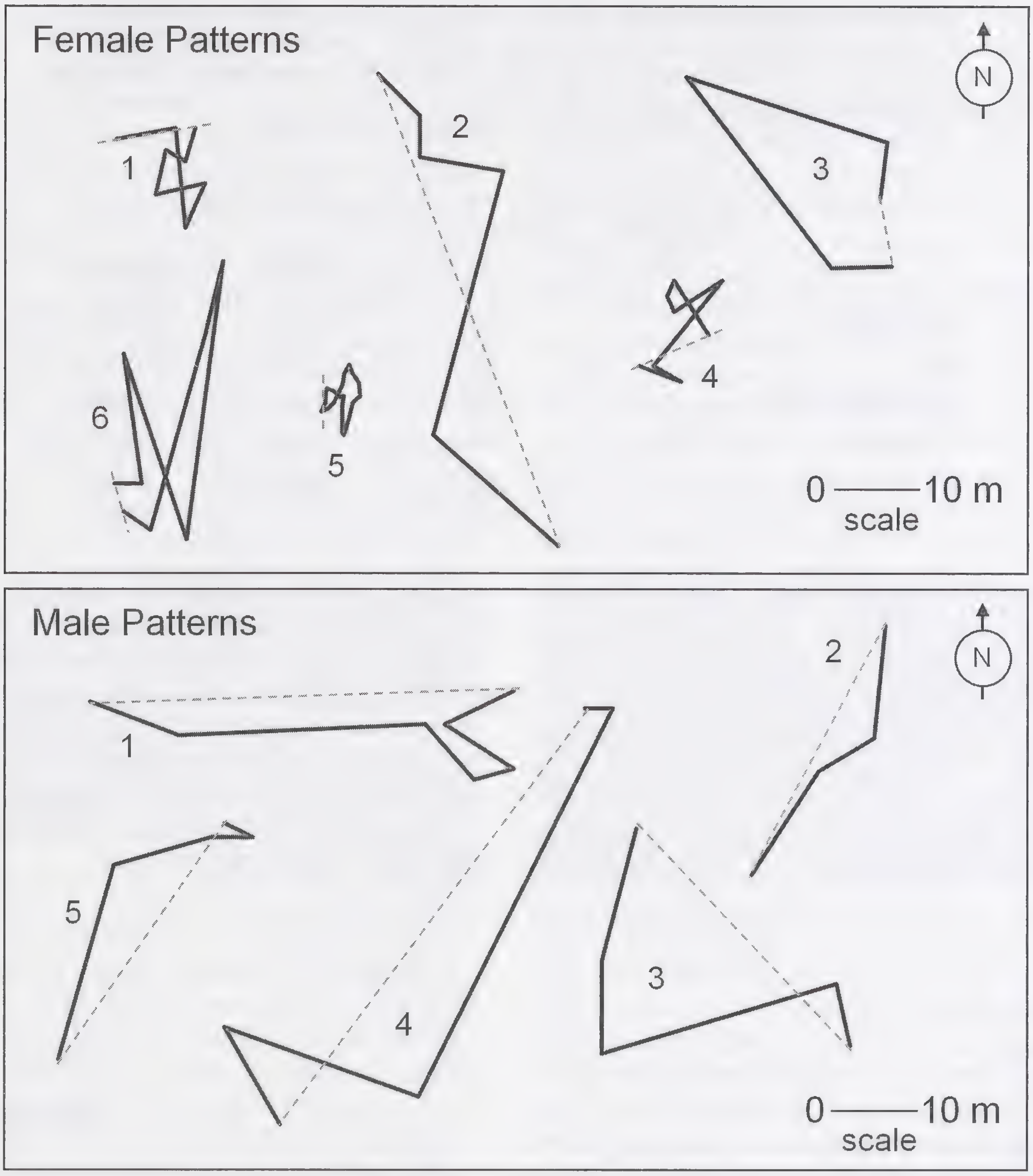

FIG. 2. Movement patterns (black solid lines) of six female (top panel) and five male snails (bottom panel) in BCWMA in 1995. Only snails for which three or more weekly movements were documented are included. Gray dashed lines intersect start and end points to show specific bearing for the Raleigh test for each snail. Vertical arrow indicates north (N). Patterns are to scale.

RESULTS

Telemetry Study

The overall average (±SD) weekly snail distance traveled was 14.8 ± 10.3 m. We found a significant difference in weekly distance traveled as a function of BWI over the 18 week period, but movement rates were not affected by gender (Table 1). However, when we partitioned the interaction effect to distinguish between male and female movements, we found no difference in distance traveled for females across BWI, but there was a significant difference for males (Table 1). Male average weekly distances varied over time with an April peak of 38 m (Fig. 1).

We found no difference in turning angles between males and females ($U^2 = 0.097$, $P > 0.1$). Five of six females did not maintain a specific bearing (Females 1, 3, 4, 5, 6, $R \leq 0.3$, $P \geq 0.14$; Female 2, $R = 0.82$, $P = 0.003$) (Fig. 2). In contrast, males were more likely to maintain a particular bearing (Males 1, 2, 3, $R \geq 0.6$, $P \leq 0.044$, Male 5, $R = 0.54$, $P = 0.066$, Male 4, $R = 0.26$, $P = 0.24$) (Fig. 2). All of these patterns included weekly movements during the April–May peak in reproduction.

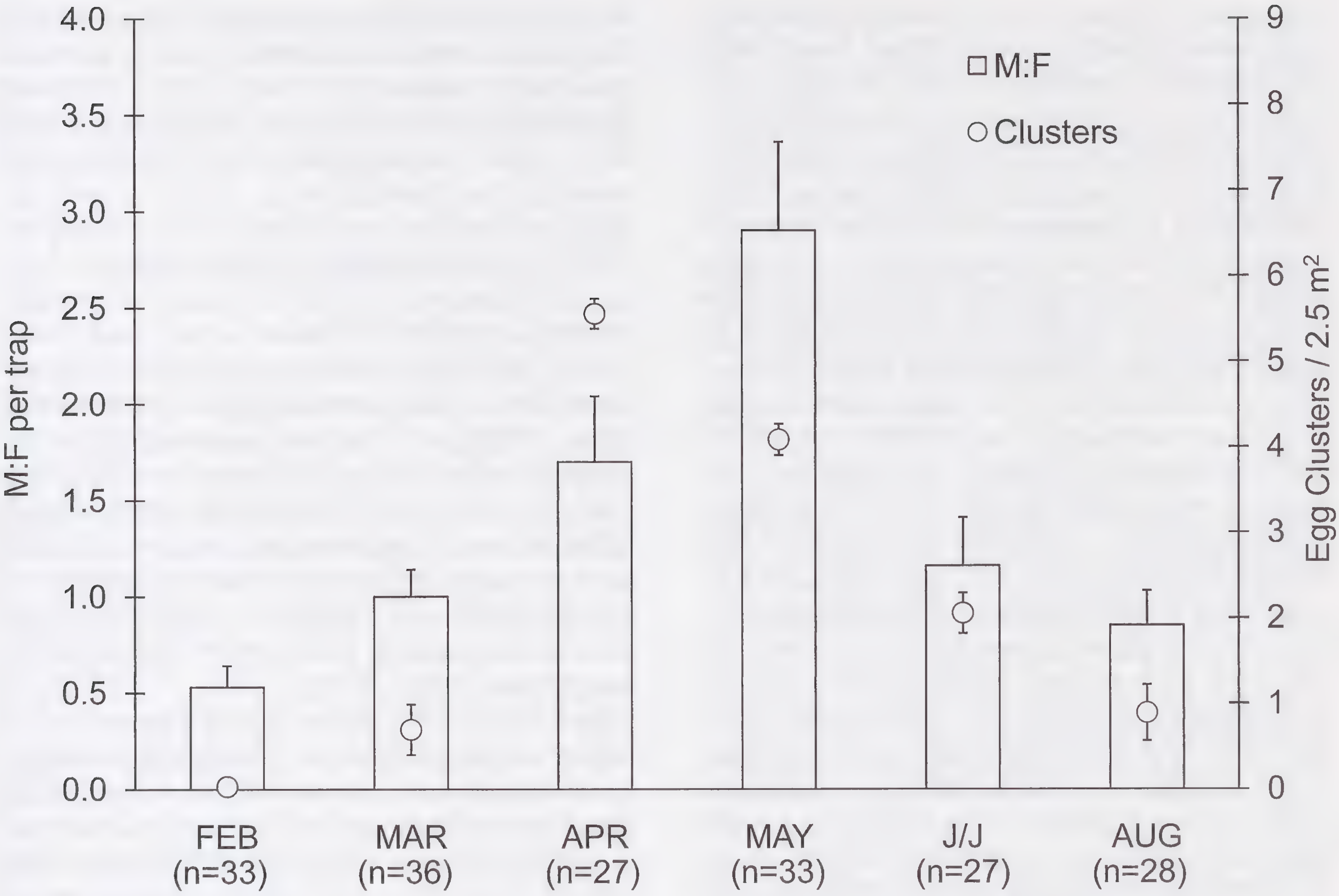

FIG. 3. M:F ratios per trap (bars) and egg clusters (circles) in BCWMA in 1996. Sample sizes in parentheses are for M:F ratios. Error bars are standard errors.

Trapping Study

A total of 846 snails were captured in the trapping study; 501 of these were males and 345 of these were females. Out of the snails randomly selected for shell measurements, female lengths were on average 38.6 ± 4.1 (SD) mm and males were 37.4 ± 3.1 mm.

Bait type (M, F, or O snail) did not affect the number of female snails or male snails captured ($\chi^2 = 1.86$, df = 2, P = 0.40 and $\chi^2 = 1.85$, df = 2, P = 0.40, respectively). There was a significant effect of trap session on the total number of females and males captured ($\chi^2 = 24.05$, df = 5, $P < 0.001$ and $\chi^2 = 130$, df = 5, $P < 0.001$, respectively). The average number of males per trap (±SD) was 0.88 ± 1.2 when no females were captured; if one or more females were in the trap, the average number of males was 2.1 ± 2.3. The M:F ratio of captured snails and egg cluster production varied over the seven month sampling period, peaking in April–May (Fig. 3). There was no linear relationship between the chronology of the trap sessions and M:F ratio ($\rho = 0.26$, P = 0.62), nor did water temperature (which was > 21°C except for February) affect the M:F ratio ($\rho = 0.52$, P = 0.29). There was a strong positive association between M:F and egg cluster counts ($\rho = 0.89$, P = 0.02). The three highest individual M:F trap ratios were 13:1 (n = 1), 8:1 (n = 1), and 6:1 (n = 3), all in April/May. We show data from only traps that had at least one F captured so we could show means and SE based on individual traps within a session (we cannot calculate a M:F ratio with zero females in the trap) (Fig. 3). However, if we look at total M:F ratio from all traps combined for each session (i.e., including traps with no females but some males), we see nearly identical M:F ratios and the same pattern (data not shown).

DISCUSSION

Florida apple snails routinely moved 15–20 m, and up to 83 m, a week. Although *Pomacea* snails can float (Burky & Burky, 1977; PCD pers. obs. in aquaria snails) and thereby potentially move with wind currents, in only one case did we observe a snail free floating during our tracking and trapping studies. We concluded that our movement data primarily represented crawling snails. When considering the distances moved, it should be noted that these distances represent a minimum distance traveled; apple snails, like other snails, unlikely move in straight lines (Tomiyama, 1992; Erlandsson & Kostylev, 1995). Like Pardo & Johnson (2004), we assumed that the weekly straight-line distances were proportional to the total non-linear distance actually traveled by snails. Although several studies of snail movements in laboratory and mesocosm studies have been conducted (e.g., Wells & Buckley, 1972; Hoffman et al., 2006), few exist for free-ranging freshwater snails. A similarly-sized freshwater snail, *Lavigeria coronata* (21–39 mm adults) moved 0.5 m/d, approximately 20 times their shell length per day (Michel et al., 2007). At 15–20 m per week (2.1–2.9 m/d), *P. paludosa* was moving approximately 50–70 times its shell length per day. Similar daily rates (2.8 m/d) were recorded for *Lanistes nyassanus* (Louda & McKaye, 1982), ampullarids similar in size to snails in our study population. Movement rates were noted for another apple snail (*Pomacea lineata*) as "several metres an hour" (Van Dinther, 1956). Ribi & Arter (1986) documented gender differences in *Viviparus ater* movement rates; 9.4 m/d for males and 4.8 m for females, distances 150 to 300 times their shell lengths.

Based on significant gender-based differences in distances traveled and movement patterns, and increased M:F ratios associated with increased egg production (and no significant effects of environmental factors), we concluded that reproduction is a major driving force for Florida apple snail movements during the breeding season. Michel et al. (2007) concluded that longer distances exhibited by male over female *Lavigeria* snails in a freshwater lake reflected mate searching. Similar gender differences in distances traveled were found for *Viviparous* snails (Ribi & Arter, 1986). Three of six groups of *Viviparous* snails released in a lake exhibited significant directional patterns in their daily movements over ten days; maintaining a bearing was associated with two groups of males in two different sites, but in a third site a Raleigh test indicated significant directionality for a group of females.

Takeichi et al. (2007) found that *P. canaliculata* males were drawn to water-borne female chemicals in the absence of slime trails in a laboratory study, but no such effect was indicated in our field study. We concluded that increased M:F ratios associated with reproductive activity reflected males tracking females that had crawled into traps. Male tracking of females via slime trails deposited during locomotion has been described for *Pomacea canaliculata* (Takeichi et al., 2007), as well as other aquatic species (Erlandsson & Kostylev, 1995). Hanning (1979) described males seeking out females, but did not study slime-trail tracking explicitly. Tracker snails have been shown to move at faster rates than marker snails (those being followed) (Erlandsson & Kostylev, 1995), and this may explain the greater distances traveled by male snails during peak breeding. For Florida apple snail males to track females over long distances, the mucous trail would presumably need to remain intact from one to several days, as has been found for other aquatic snails (Davies & Williams, 1995; Hutchinson et al., 2007).

Gender differences in movement may reflect investment-based reproductive strategies to maximize fitness. Ribi & Arter (1986) described male snails as investing more (relative to females) in movements because they benefit more from increasing potential mate encounters. In contrast, females require fewer matings to achieve maximum fitness potential (which may be constrained by the ability to produce eggs) and consequently move less. Hanning (1979) described incidences of female *P. paludosa* snails being unreceptive to mating, and actively dislodging males attempting to mate. Similar observations have been made for *P. canaliculata* (Burela & Martin, 2009). Each of these observations in *Pomacea* was consistent with the idea that females gain less from additional matings. In a case of a conditional strategy, Tomiyama (1992) concluded that longer more linear movements by young adult sperm-producing land snails (*Achatina fulica*) reflected the need to find egg-producing mates. Older *A. fulica* produce both sperm and eggs, lessening the need for investing in mate finding, so they traveled shorter distances (Tomiyama, 1992).

Movements by Florida apple snails were influenced by gender and reproductive status during their reproductive season. Their ability to routinely move 10–20 m per week and track mates over long distances may be critical for a species that tends to occur at relatively low densities (often < 0.2 snails/m^2), compared to other freshwater gastropods that often occur at dozens or hundreds of individuals per m^2 (Strzelec & Krolczyk, 2004; Jakubik, 2007;

Clark et al., 2008). Additional studies would be required to determine whether trail-following is the mechanism behind the gender differences in movements and changes in M:F ratios found in passive traps that we observed.

ACKNOWLEDGEMENTS

The field project was funded by the South Florida Water Management District (West Palm Beach, Florida) and the St. Johns River Water Management District (Palatka, Florida) through a contract with the Florida Cooperative Fish and Wildlife Research Unit (Gainesville, Florida). Research support was also provided to PCD by the Department of Biology and College of Arts and Sciences at the University of West Florida (Pensacola, Florida). Bethany Wight (UWF) provided valuable assistance in manuscript preparation. We thank Ikuko Fujisaki (University of Florida) for help with statistical analyses. We thank Chris Cattau (UF), Charles D'Asaro (UWF), and three anonymous reviewers for helpful comments on drafts of this manuscript.

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Revised ms. accepted 5 February 2011

MALACOLOGIA, 2011, 54(1–2): 119–138

THE GENUS *CUSPIDARIA* (PELECYPODA: SEPTIBRANCHIA: CUSPIDARIIDAE) FROM THE DEEP SEA OF CAMPOS BASIN, BRAZIL, WITH DESCRIPTIONS OF TWO NEW SPECIES

Ricardo Silva Absalão & Cléo Dilnei De Castro Oliveira*

Departamento de Zoologia, Instituto de Biologia, Centro de Ciências da Saúde,
Universidade Federal do Rio de Janeiro, Ilha do Fundão, 21941-590 Rio de Janeiro, Brazil

ABSTRACT

A revision of the members of *Cuspidaria* present on the continental slope (700–2,000 m) of the Campos Basin (22°S) off southeastern Brazil was carried out. Eight taxa are recognized. Two of them were previously unknown to science and are described here: ***Cuspidaria tamandua***, n. sp., and ***Cuspidaria wapixana***, n. sp. Three species are recorded from Brazilian waters for the first time: *Cuspidaria papyria* Jeffreys, 1876, a poorly described species that is here redescribed; *Cuspidaria wollastonii* Smith, 1885; and *Cuspidaria* cf. *barnardi* Knudsen, 1970. The geographic distribution is enlarged northwards for *Cuspidaria platensis* (Smith, 1885) and southwards for *Cuspidaria monosteira* Dall, 1890. *Cuspidaria circinata* (Jeffreys, 1876) was previously reported for Brazil, but the present record fills a gap in its distribution in the southwest Atlantic. *Bathyneaera globulosa* Krylova, 1993, is here considered a junior synonym of *C. monosteira*; *Cuspidaria consociata* (Smith, 1885) and *Cuspidaria munieri* Dautzenberg & Fischer, 1897, are both considered junior synonyms of *C. circinata*. A list of all *Cuspidaria* species recorded for the Atlantic Ocean is given.

Key words: Pelecypoda, Septibranchia, Cuspidariidae, *Cuspidaria*, biodiversity, Brazil.

INTRODUCTION

The Cuspidariidae are often found in the deep sea, and are one of the largest families of pelecypods in this environment in the Atlantic Ocean (Allen, 2008: 59). The shell is thin and small, about 10 mm long, although larger species are known (e.g., *Cuspidaria wollastonii* Smith, 1885). The outline is strongly inequilateral, usually very rostrate, and the hinge is typically edentulous or has secondary teeth.

Knowledge of the number of species in this family grew rapidly in the 19th and 20th centuries, and several Recent species have been described for the Atlantic Ocean. Nevertheless, despite the importance of the Cuspidariidae in the deep sea and efforts of several authors (e.g., Jeffreys, 1881; Smith, 1885; Dall, 1886; Verrill & Bush, 1898; Knudsen, 1970, 1982, 2005; Allen & Morgan, 1981; Krylova, 1993, 1994, 1995; Poutiers & Bernard, 1995; Oliveira & Absalão, 2009), the taxonomy of this family is still poorly resolved. As part of a continuing effort to contribute to knowledge of the taxonomy of the deep sea septibranchs, this article describes the results of a taxonomic revision of the genus *Cuspidaria*, family Cuspidariidae, from the Campos Basin off Rio de Janeiro state, Brazil.

MATERIALS AND METHODS

The samples were taken on the continental slope of Brazil, Rio de Janeiro state, off Campos Basin (22°S, 41°W), at depths from 700 to 1,950 m, between 2001 and 2003. The samples were taken with a 0.25 m^2 box corer, from the Research Vessel "Astro-Garoupa" as part of the program "Environmental Characterization of Campos Basin, RJ, Brazil" under the auspices of PETROBRAS S.A.

Each sample was washed through a 0.5 mm mesh, and preserved in 70% ethanol. Most of the shells were in a good state of conservation, but no live specimens were found. Each species was photographed under a scanning electron microscope (ZEISS EVO 40), at the Gerência de Bioestratigrafia e Paleoecologia Aplicada (BPA), of the Petrobrás Research Center (Centro de Pesquisas da Petrobrás – CENPES).

*Corresponding author: cleo.oliveira@gmail.com

In most cases, the original illustration and/or description were sufficient to identify the taxon. When they were not, we compared our specimens against the types and other specimens deposited in: The Natural History Museum, London (NHMUK), Musée Océanographique de Monaco (MOM), Smithsonian National Museum of Natural History (USNM), and Zoological Museum of Moscow State University (ZMMU).

For each species treated here, under *Distribution*, only those authors who increased the known geographical distribution are included. Authors who merely repeated previous records are not cited.

The specimens from the present study are deposited in the Mollusca collection of the following institutions: Departamento de Zoologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ), Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Museu de Zoologia, Universidade de São Paulo (MZSP), Museu Oceanográfico "Prof. Eliezer Rios" Universidade Federal do Rio Grande (MOFURG), Muséum National d'Histoire Naturelle, Paris (MNHN) and Museum of Comparative Zoology, Harvard University (MCZ).

RESULTS AND DISCUSSION

Family Cuspidariidae Dall, 1886

Type Genus: *Cuspidaria* Nardo, 1840 (synonym: *Neaera* Gray, 1834).

Diagnosis: Shell medium-sized, usually thin, inequilateral, rounded anteriorly, posterior margin usually with a strong rostrum. Slightly inequivalve, left valve larger. External ornamentation variable: smooth, granulated, or commarginally and/or radially ornamented. Hinge feeble, resilifer small, teeth absent or secondarily present. Description adapted from Dall (1886), Keen (1969), Allen & Morgan (1981) and Poutiers & Bernard (1995).

Remarks: Most taxa now placed in the family Cuspidariidae were once allocated to other families (e.g., Corbulidae Lamarck, 1818, and Myidae Lamarck, 1809). After the work of Smith (1885), Dall (1886) described the new family Cuspidariidae, also proposing new taxa (e.g., *Myonera* Dall & Smith, 1886) and transferring other previously known taxa to this new family (e.g., *Cuspidaria*; *Cardiomya* A. Adams, 1864). Several new genera have been described more recently (e.g., *Octoporia* Scarlato & Starobogatov, 1983; *Protocuspidaria* Allen & Morgan, 1981). However, the phylogenetic relationships among them remain poorly resolved (Oliveira & Absalão, 2009), and the genera are in need of reevaluation.

Genus *Cuspidaria* Nardo, 1840

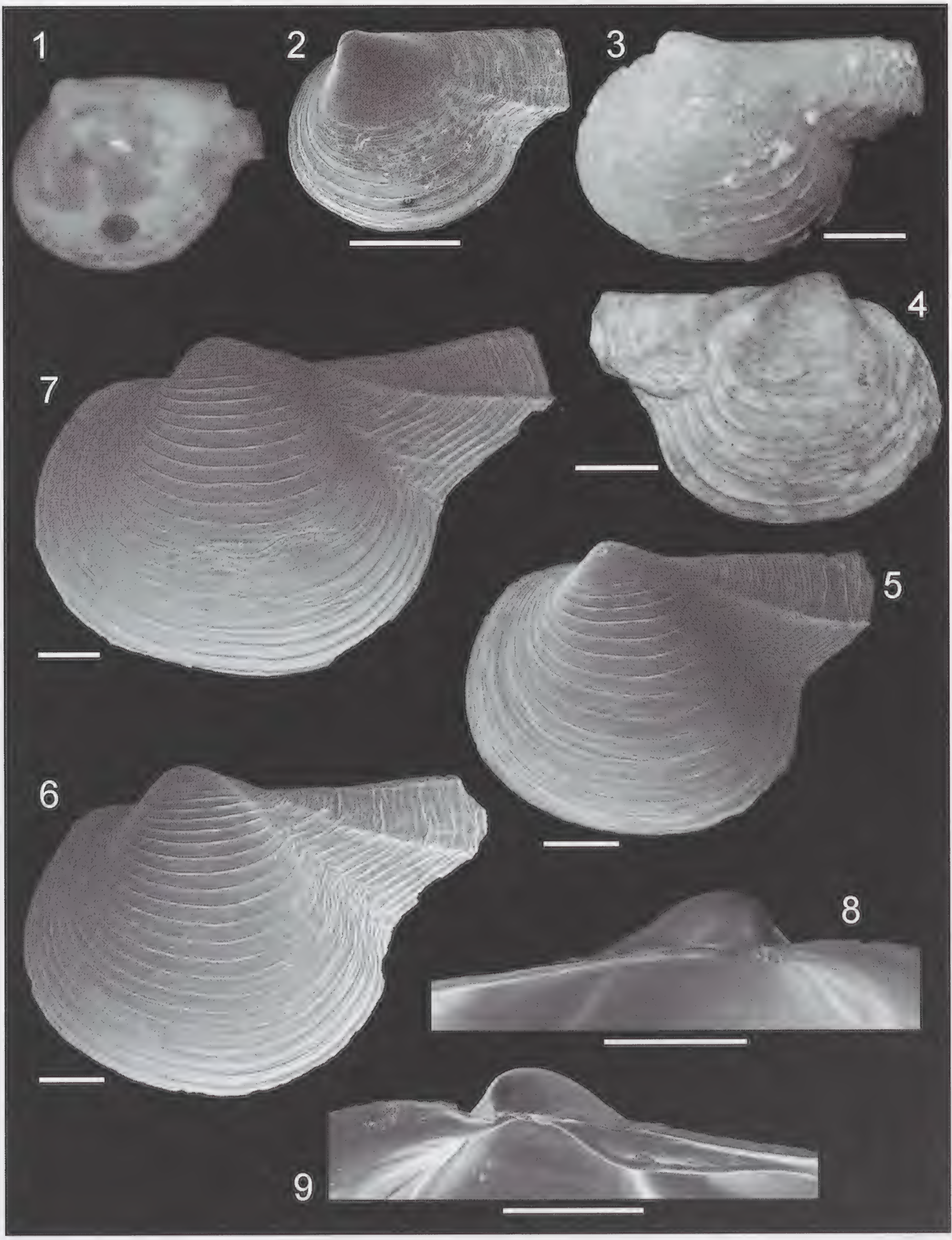
Type Species: *Tellina cuspidata* Olivi, 1792, a senior synonym of *Cuspidaria typus* Nardo, 1840, by monotypy.

The heterogeneity and the morphological diversity among species now included in *Cuspidaria* surpass the limits imposed by the current concept of this genus. For this reason, we have adapted the generic diagnosis below in order to allow the accommodation of most of the known species of the genus until a formal complete revision is conducted.

Diagnosis: Shell thin, slightly convex, slightly inequivalve, left valve usually larger. Inequilateral, posteriorly rostrate, rostrum length variable. Externally ornamented, usually by commarginal striae, lines, or cords; a primary and secondary rostral ridge may be present. Hinge feeble, resilifer small, teeth absent or present at least on right valve. Diagnosis adapted from Nardo (1840), Dall (1886), Keen (1969), Allen & Morgan (1981), Poutiers & Bernard (1995).

Remarks: This genus has a somewhat complicated history since the first *Cuspidaria* species were described in *Neaera* Gray, 1839. Later, Nardo (1840) established the genus *Cuspidaria*, a junior synonymy of *Neaera* Gray; however, the name *Neaera* Gray proved to be preoccupied by *Neaera* Robineau-Desvoidy, 1830 (Diptera). Dall (1886) was the first one to deal with this problem and, because the *Neaera* was preoccupied, he transferred its species to *Cuspidaria*.

This is the largest genus in Cuspidariidae, with more than a hundred described species and several different proposals for the subgeneric classification, most of them based on hinge features (e.g., presence or absence of teeth at right valve) and shell ornamentation (e.g., presence or absence of commarginal or radial ribs). On the other hand, several groups recently treated at generic level among cuspidariids, were previously recognized as subgenera or sections of *Cuspidaria* (e.g., *Cardiomya*; *Leiomya* A. Adams, 1864). More-



FIGS. 1–9. *Cuspidaria circinata* (Jeffreys, 1876), growth series. FIG. 1: *Cuspidaria consociata* (Smith, 1885), type (NHMUK 2003.0607); FIG. 2: *C. circinata*, ordinary specimen (IBUFRJ 18822); FIG. 3: *Cuspidaria munieri* Dautzenberg & Fischer, 1897, type (MOM); FIG. 4: *C. circinata*, type (USNM 63961); FIG. 5: *C. circinata*, ordinary specimen (IBUFRJ 18818); FIG. 6: *C. circinata*, ordinary specimen(IBUFRJ 18824); FIG. 7: *C. circinata*, ordinary specimen (IBUFRJ 18815); FIG. 8: *C. circinata*, ordinary specimen (IBUFRJ 18823); FIG. 9: *C. circinata*, ordinary specimen (IBUFRJ 18813). Scale bars: FIG. 1 no scale; FIGS. 2–9 = 1 mm.

over, there are species originally described in the genus *Cuspidaria* but considered in another combination later. For instance, *Cuspidaria acutecarinata* Dautzenberg & Fischer, 1906, and *Cuspidaria centobi* Bouchet & Warén, 1979, are now allocated to *Myonera*. To avoid confusion, we are using only the genus *Cuspidaria* for the deep Atlantic Ocean species and, for the authors who have used subgeneric classification, only those species included in the subgenus *Cuspidaria s.s.*

There are 51 know species of *Cuspidaria* previously recorded in the Atlantic Ocean: *C. cuspidata* (Olivi, 1792); *C. rostrata* (Spengler, 1793); *C. obesa* (Lovén, 1846); *C. jugosa* (S. V. Wood, 1850); *C. pellucida* (Stimpson, 1853); *C. arctica* (M. Sars, 1859); *C. papyria* (Jeffreys, 1876); *C. exigua* (Jeffreys, 1876); *C. circinata* (Jeffreys, 1876); *C. subtorta* (G. O. Sars, 1878); *C. lamellosa* (G. O. Sars, 1878); *C. glacialis* (G. O. Sars, 1878); *C. arcuata* (Dall, 1881); *C. jeffreysi* (Dall, 1881); *C. sulcifera* (Jeffreys, 1882); *C. gracilis* (Jeffreys 1882); *C. bicarinata* (Jeffreys, 1882); *C. contracta* (Jeffreys, 1882); *C. undata* (Verrill, 1884); *C. consociata* (Smith, 1885); *C. azorica* (Smith, 1885); *C. capensis* (Smith, 1885); *C. kerguelensis* (Smith, 1885); *C. wollastonii* (Smith, 1885); *C. platensis* (Smith, 1885); *C. microrhina* Dall, 1886; *C. monosteira* Dall, 1890; *C. maxima* Dautzenberg & Fischer, 1897; *C. munieri* Dautzenberg & Fischer, 1897; *C. formosa* Verrill & Bush, 1898; *C. fraterna* Verrill & Bush, 1898; *C. media* Verrill & Bush, 1898; *C. ventricosa* Verrill & Bush, 1898; *C. turgida* Verrill & Bush, 1898; *C. parva* Verrill & Bush, 1898; *C. semirostrata* Locard, 1898; *C. imbricata* (Locard, 1898); *C. tenella* Smith, 1907; *C. plicata* Thiele, 1912; *C. concentrica* Thiele, 1912; *C. infelix* Thiele, 1912; *C. braziliensis* Smith, 1915; *C. guineensis* Knudsen, 1970; *C. barnardi* Knudsen, 1970; *C. atlantica* Allen & Morgan, 1981; *C. multicostata* Egorova, 1993; *C. minima* (Egorova, 1993); *C. smirnovi* Egorova, 1998; *C. luymesi* Knudsen, 2005; *C. altenai* Knudsen, 2005; *C. meteoris* Krylova, 2006.

From all these species, only six were previously registered for Brazil: *C. monosteira* (by Dall, 1890), *C. braziliensis* (by Smith, 1915), *C. parva* and *C. circinata* (both by Allen & Morgan, 1981), *C. platensis* (by Figueiras & Sicardi, 1980), *C. rostrata* (by Rios, 1994). Among them, *C. braziliensis* must be re-allocated in genus *Plectodon* Carpenter, 1864, because it has an external surface covered by small granules (Pimpão et al., 2010).

Cuspidaria circinata (Jeffreys, 1876)
(Figs. 1–13)

Neaera circinata Jeffreys, 1876: 497–498.
Neaera circinata: Jeffreys (1881: 942, pl. 71, fig. 6); Smith (1885: 42, pl. 10, fig. 4–4b).
Cuspidaria circinata: Dautzenberg (1889: 87); Dautzenberg & Fischer (1897: 222); Locard (1898: 185; 1899: 128); Dautzenberg (1927: 338); Allen & Morgan (1981: 459–460, fig. 25); Poutiers & Bernard (1995: 149, 158); Salas (1996: 74, figs. 125–126); Scarabino (2003: 238); Allen (2008: 79, 113, 117, 120).
Neaera consociata Smith, 1885: 41, pl. 9, fig. 7, 7b.
Cuspidaria consociata: Knudsen (1982: 131–132, 138, figs. 10, 11); Poutiers & Bernard (1995: 149, 158).
Cuspidaria munieri Dautzenberg & Fischer, 1897: 225–226, pl. 7, figs. 5, 6.
Cuspidaria munieri: Dautzenberg (1927: 339, pl. 9, figs. 5, 6).

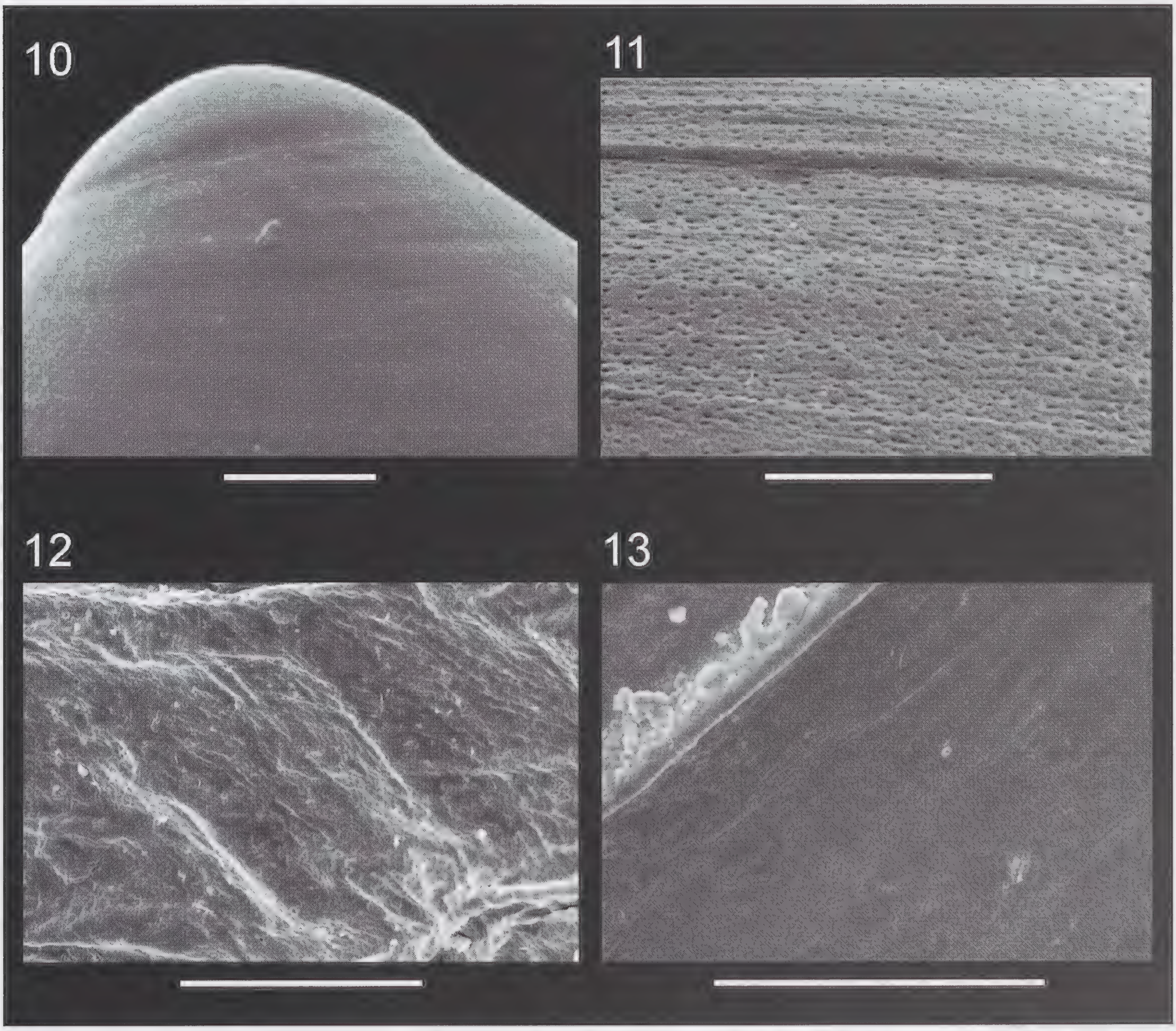
Description: Shell white, small (height, 1.5–5.5 mm; length, 2.5–9.0 mm), elongate, inequivalve, inequilateral, rostrate, very convex, umbo large, prosogyric. Rostrum slender, long. Posterior margin straight, posteroventral sinuation marked, ventral and anterior margins rounded, anterodorsal margin forming a shoulder. Externally ornamented usually by up to 15 commarginal cords and countless growth lines; rostrum with two rostral ridges, one diagonal and another almost parallel to posterodorsal margin. Micropits present only on the interdissoconch. Hinge of left valve edentulous, right valve with strong posterior teeth. Resilífer slender, deep.

Type Locality: SE of Greenland, "Valorous" Expedition, sta. 12 (56°11'N, 37°41'W), 2,652 m, off Portugal, "Porcupine" Expedition 1870, sta. 16 (39°55'N, 9°56'W), 1,818 m.

Distribution: Atlantic Ocean: northwestern Atlantic: SE of Greenland (Jeffreys, 1876); off Bermuda, NE of Culebra Island, West Indies (Smith, 1885); Saba Bank (Knudsen, 1982). Southwestern Atlantic: Brazil: off Pernambuco (Allen & Morgan, 1981); off Campos Basin, Rio de Janeiro state (present study). Off Uruguay (Allen & Morgan, 1981). Northeastern Atlantic: off Isla de la Palma, Canary Islands (Smith, 1885); W of Marroc (Locard, 1898); W of the Strait of Gibraltar (Salas, 1996); off Portugal (Jeffreys, 1876, 1881); Azores and W of Azores (Jeffreys, 1881;

Smith, 1885; Dautzenberg & Fischer, 1897); Bay of Biscay (Jeffreys, 1881; Locard, 1898; Allen & Morgan, 1981); SE of Ireland (Allen & Morgan, 1981); NW of Ireland (Jeffreys, 1881). Bathymetry: from 340 m (Knudsen, 1982) to 4,382 m (Allen & Morgan, 1981).

Material Examined: IBUFRJ 18812 (22°09'10"S, 39°44'50"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18813 (22°11'16"S, 39°43'44"W, 1,950 m), 25.XI.02 [1valve]; IBUFRJ 18814 (22°46'59"S, 40°07'49"W, 1,650 m), 22.XI.02 [1 valve]; IBUFRJ 18815 (22°41'35"S, 40°00'45"W, 1,950 m), 22.XI.02 [1 valve]; IBUFRJ 18816, (22°31'28"S, 40°03'50"W, 1,050 m), 19.XI.02 [1 valve]; IBUFRJ 18817 (22°24'31"S, 39°57'28"W, 1,050 m), 20.XI.02 [1 valve]; IBUFRJ 18818 (22°11'16"S, 39°43'44"W, 1,950 m), 22.VI.03 [1 valve]; IBUFRJ 18819 (22°04'45"S, 39°41'58"W, 1,950 m), 27.VI.03 [1 valve]; IBUFRJ 18820 (21°52'59"S, 39°55'32"W, 750 m), 29.VI.03 [3 valves]; IBUFRJ 18821 (22°41'31"S, 40°00'47"W, 1,950 m), 06.XII.03 [1 valve]; IBUFRJ 18822 (22°31'28"S, 40°03'49"W, 1,050 m), 18.VI.03 [1 valve]; IBUFRJ 18823 (22°37'02"S, 39°56'20"W, 1,950 m), 13.VI.03 [1 valve]; IBUFRJ 18824 (22°31'37"S, 39°55'14"W, 1,650 m), 16.VI.03 [2 valves]; *C. consociata*: types: NHMUK 2003.0607, off Bermuda, 795 m; NHMUK 1887.2.9.2406-7, off Culebra Island, West Indies, 713 m, destroyed by Byne's disease; *C. munieri*: type: MOM, off Azores, 1,846 m; *C. circinata*: type: USNM 63960, NW of Ireland, 1,214 m, fragmented; USNM 63961, off Portugal, 1,818 m.



FIGS. 10–13. *Cuspidaria circinata* (Jeffreys, 1876). FIG. 10: IBUFRJ 18822, punctate surface towards the umbo; FIG. 11: IBUFRJ 18823, interdissoconch with micropits; FIGS. 12, 13: IBUFRJ 18813, rostrum and anterior margin details, respectively. Scale bars = 100 µm.

Discussion: *Cuspidaria circinata* varies in outline during its ontogeny. The shell becomes more convex, and the prodisso- and the interdissoconch become progressively more enclosed and eventually hidden by the teleoconch, and the anterior margin becomes more rounded and prominent. Because the micropits are restricted to the interdissoconch, in adult specimens, they are visible only at the top of the shell. We have been able to examine the type specimens of *C. consociata* in the British Museum [NHMUK 1887.2.9.2406-7, destroyed by Byne's disease], and an additional preserved specimen [NHMUK 2003.0607] that is a very good fit to the concept of this species.

The preserved specimen (Fig. 1) of *C. consociata* is very similar to the young stages of *C. circinata,* and also, as noted by Smith (1885: 41), *C. consociata* "presents a minutely punctate surface towards the umbo, both within and without". At this time, we regard Smith's specimens "without punctate surface" as an effect caused by observation through optical microscopy, because, in observing our material under an optical microscope, we did not see the micropits in some specimens (Oliveira & Absalão, 2009), although it was visible under scanning electron microscopy. Therefore, since *C. consociata* shows no differences from the young stages of *C. circinata,* and additionally, considering the change in outline and external ornamentation observed for *C. circinata*, we consider these two species to be synonyms.

The specimen illustrated as *C. consociata* by Knudsen (1982: figs. 10, 11) has a longer posterior lateral tooth on the right valve. At this time, we consider this difference to be an individual variation.

Cuspidaria munieri Dautzenberg & Fischer, 1897, described based on a single left valve with an edentulous hinge, from the Azores at 1,846 m, is also quite similar to *C. circinata*, an opinion shared with Allen & Morgan (1981: 459). After examining a photograph of the type specimens of *C. munieri* (Fig. 3), and considering the variation in the growth series of our specimens, we propose this latter species as a junior synonym of *C. circinata*.

Cuspidaria circinata can be distinguished from two other similar Atlantic commarginally ornamented species, *C. concentrica* and *C. minima*, in the presence in *C. circinata* of a marked posteroventral sinuation, a longer dorsoventral axis, and a well-developed hinge plate on the anterior region, which forms a shoulder at the anterodorsal margin viewed externally. Such features are absent in *C. concentrica* and *C. minima.* Both species have a more elongate outline, a less-marked posteroventral sinuation, and no hinge plate developed on the anterior side. *Cuspidaria minima* also differs from *C. circinata* in the presence of a posterior lateral tooth on the left valve of the former.

Cuspidaria (?) *monosteira* Dall, 1890
(Figs. 14–23)

Cuspidaria (?) *monosteira* Dall, 1890: 281, pl. 8, fig. 5.

Verticordia monosteira: Knudsen (1982: 126, figs 2, 3); Poutiers & Bernard (1995: 142, 163).

Bathyneaera globulosa Krylova, 1993: 55, fig. 1I–L.

Cuspidaria monosteira: Rios (1994: 303, fig. 1480; 2009: 605, fig. 1675).

Description: Shell white, small (height, 3.7 mm; length, 3.8 mm), triangular, inequilateral, rostrate, very convex, umbo large, central. Rostrum short. Posterodorsal margin strongly oblique, descending, posteroventral sinuation marked, confined by the rostral ridge and by a strong radial keel extending from the umbo to the lower point of the "V"-shaped ventral margin, anteroventral margin slightly curved upwards, anterodorsal margin almost vertical. Externally ornamented with several commarginal growth lines and incomplete commarginal ribs on anterior margin, these ribs more pronounced near anteroventral margin. Micropits absent. Hinge edentulous, left valve with a projection of the posterior hinge plate. Resilifer triangular, deep.

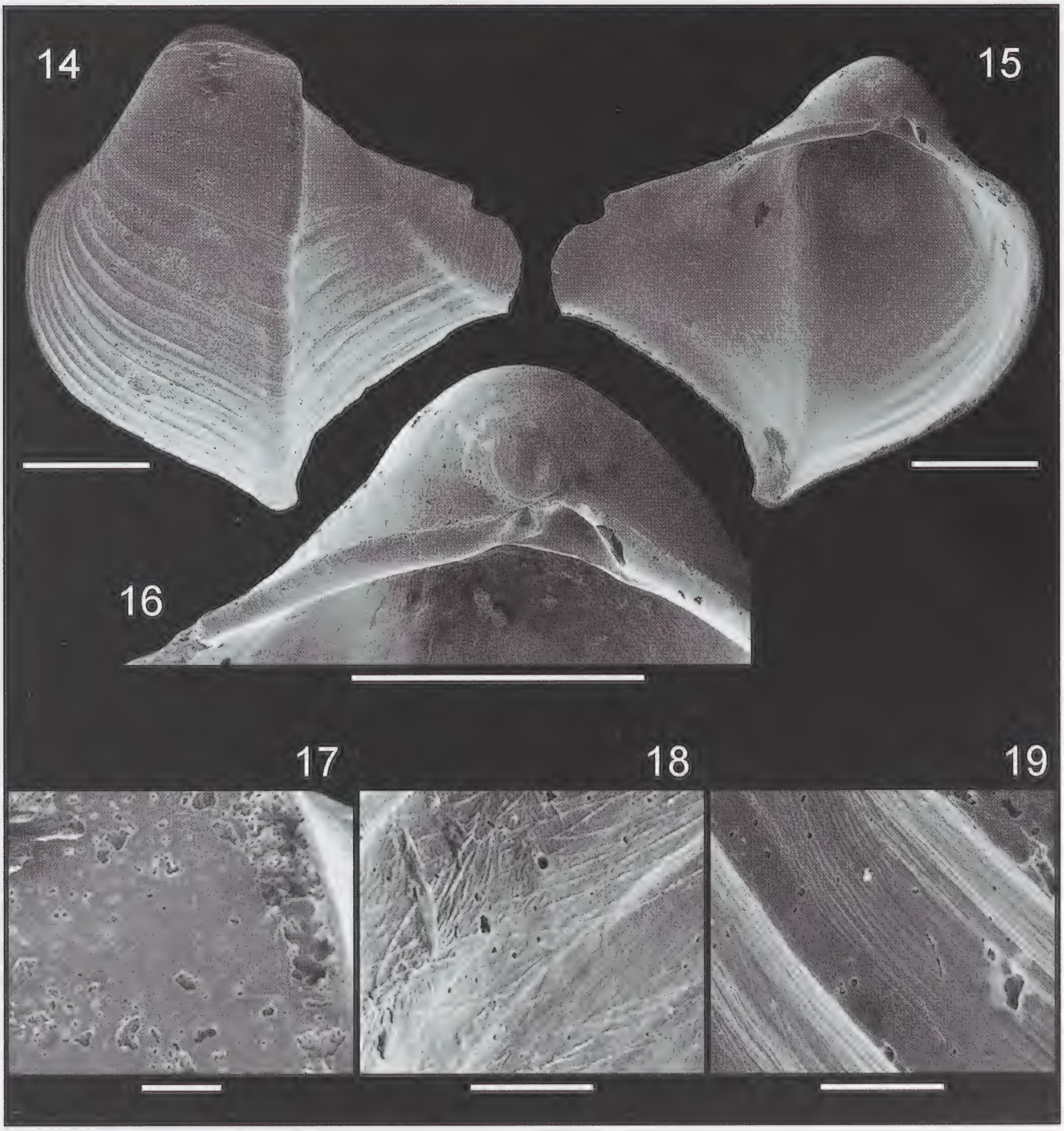
Type Locality: U.S. Fish Commission sta. 2760, off north of Bahia, Brazil (12°7'S, 37°17'W, 1,864 m).

Distribution: Atlantic Ocean: northwest Atlantic: E of Yakutat Seamount (Krylova, 1993). Saba Bank (Knudsen, 1982). Southwest Atlantic: Brazil: N of Bahia (Dall, 1890), off Campos Basin, Rio de Janeiro state (present study). Bathymetry: from 850 m (Knudsen, 1982) to 4,480 m (Krylova, 1993).

Material Examined: IBUFRJ 18772 (21°58'36"S, 39°46'30"W, 1,700 m), 08.X.01 [1 valve]; *C. monosteira*: Holotype: USNM 95457 (type locality); *B. globulosa*: Holotype: ZMMU 2860, east of Yakutat Seamount, 4,440–4,480 m.

Discussion: This very rare species, with only two valves under the name *C. monosteira* previously reported in the literature (i.e., Dall, 1890; Knudsen, 1982), was wrongly reported in the original description as “90 miles north from Ceara” but the coordinates actually indicate a location off the state of Bahia, Brazil. This error was followed by subsequent authors (e.g., Rios, 2009).

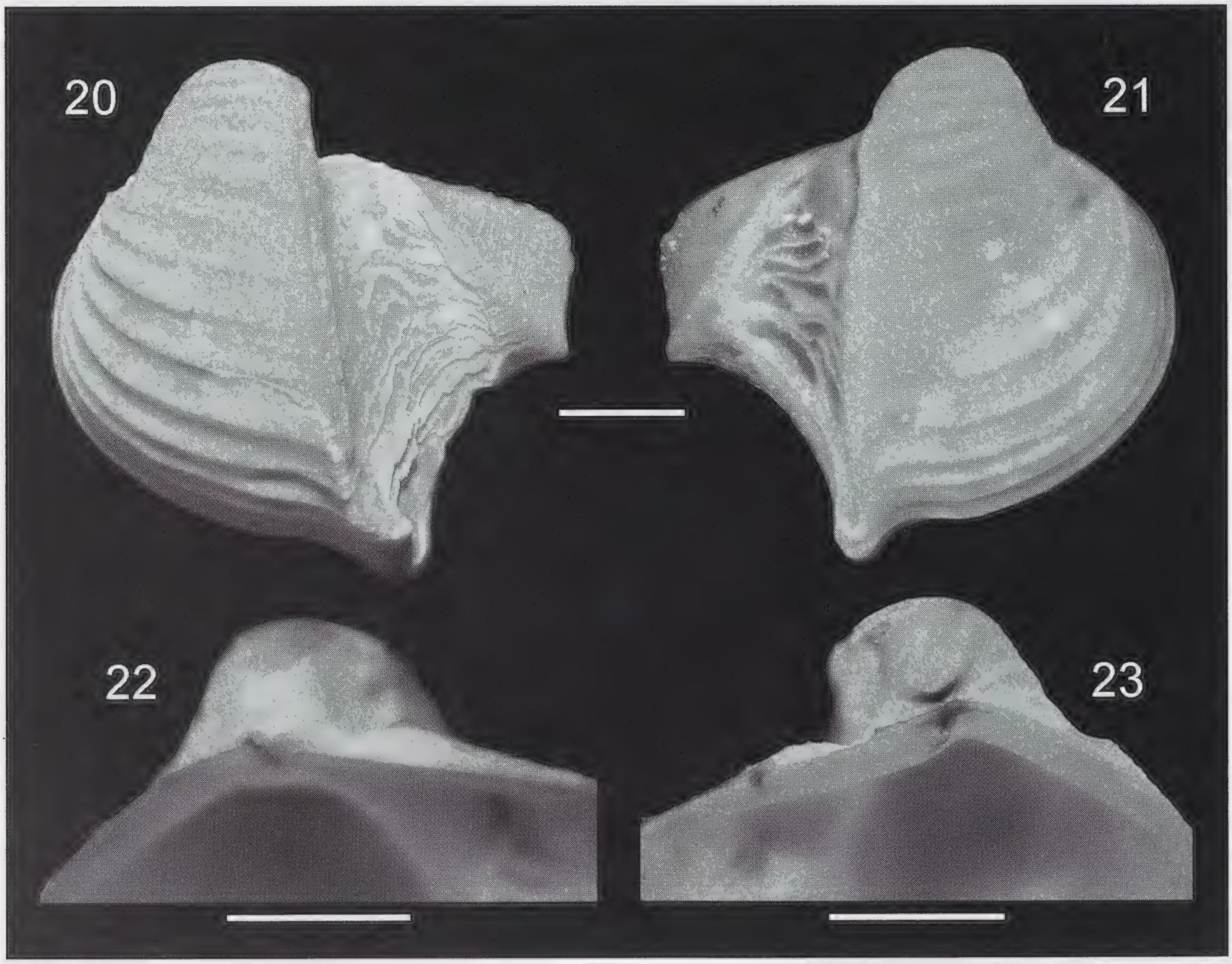
As reported by Krylova (1993: 55), *Bathyneaera globulosa* Krylova, 1993, and *C. monosteira* are conchologically very similar, the diagnostic character being the absence of hinge teeth in the former. Upon initial examination, *C. monosteira* appears to have a long “posterior lateral tooth”, as described by Dall (1890: 281), but actually this seems to be merely a concave projection of the hinge plate, not a real tooth (Fig. 16). We have been able to examine the type specimen of *B. globulosa* (Figs. 20–23). It agrees perfectly with the concept of *C. monosteira*, and the



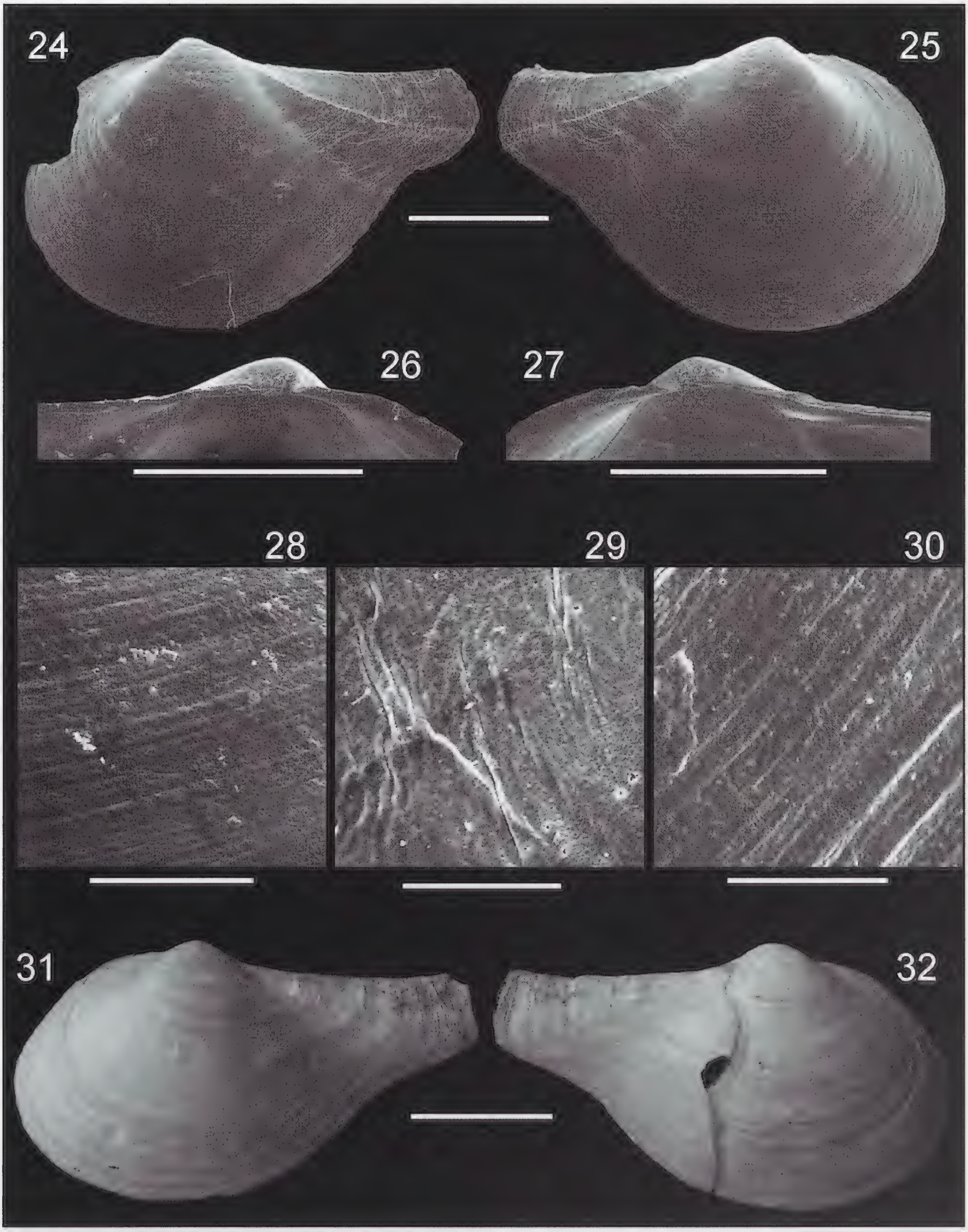
FIGS. 14–19. *Cuspidaria monosteira* Dall, 1889, IBUFRJ 18772. FIGS. 14, 15: External and internal view; FIG. 16: Hinge detail; FIGS. 17–19: Umbo, rostrum and anterior margin details, respectively. Scale bars: FIGS. 14–16 = 1 mm, FIG. 17 = 200 µm, FIGS. 18, 19 = 100 µm.

"absence of tooth" attributed to *B. globulosa* is caused merely by a thicker posterior hinge plate, which eliminates the concave appearance. Thus, the "presence" or "absence" of the posterior tooth may be regarded as a simple variation in the thickness of the hinge plate, and therefore we consider *B. globulosa* to be a junior synonym of *C. monosteira*.

The presence of *C. monosteira,* a very distinct species, in the genus *Cuspidaria* requires particular discussion. This species shows characteristics of several different genera, and it is difficult to convincingly allocate it to any currently valid genus. Dall (1890: 281) made clear his doubts about this subject when he utilized the symbol "?" in the description of *C. monosteira*. Knudsen (1982: 126) allocated *C. monosteira* to the genus *Verticordia* Sowerby, 1844; however, "the presence of a rostrum at the posterior margin and two radial keels, as well as the absence of a lunule [...] do not support the allocation of this species to the genus *Verticordia.*" (Oliveira & Absalão, 2010: 811). Krylova (1993: 55) allocated *B. globulosa* (a junior synonym of *C. monosteira*) to the genus *Bathyneaera*, but this species has two very strong radial keels that interrupt the more-or-less-continuous outline observed for the genus *Bathyneaera;* and additionally, the concept of this genus states that all members should be elliptical in outline with an external surface adorned by a mesh of commarginal and radial ornamentation – characters that are absent in *B. globulosa*. Thus, considering that the creation of new supraspecific taxa in a group (Cuspidariidae) that is still poorly taxonomically resolved would be worthless, we opt to provisionally retain *C. monosteira* in its original combination.



FIGS. 20–23. *Bathyneaera globulosa* Krylova, 1993, holotype (ZMMU 2860). FIG. 20: External view, left valve; FIG. 21: External view, right valve; FIGS. 22, 23: Hinge details, right and left valve, respectively. Scale bars = 1 mm.



FIGS. 24–30. *Cuspidaria platensis* (Smith, 1885), IBUFRJ 18777. FIG. 24: External view, left valve; FIG. 25: External view, right valve; FIGS. 26, 27: Hinge details, left and right valve, respectively; FIGS. 28–30: Umbo, rostrum and anterior margin details, respectively; FIGS. 31, 32: *Cuspidaria platensis* (Smith, 1885), type (NHMUK 1887.2.9.2417). Scale bars: FIGS. 24–27 = 2 mm, FIGS. 28–30 = 100 µm, FIGS. 31, 32 = 4 mm.

Cuspidaria platensis (Smith, 1885)
(Figs. 24–32)

Neaera platensis Smith, 1885: 45, pl. 9, fig. 4–4b.
Cuspidaria platensis: Figueiras & Sicardi (1980: 156–157, pl. 2, fig. 19); Rios (1994: 303, pl. 104, fig. 1481); Poutiers & Bernard (1995: 149, 165); Scarabino (2003: 238).

Description: Shell white, small (height, 2–4 mm; length, 3–6 mm), elongate, inequivalve, inequilateral, rostrate, convex. Umbo large, prosogyrate. Rostrum long. Posterodorsal margin slightly curved upwards, posteroventral sinuation little marked, ventral and anterior margin rounded, anterodorsal margin slightly extended horizontally just after the umbo. Externally ornamented with indistinct commarginal growth lines, rostral ridge may be present, few radial striae present on rostrum. Micropits absent. Hinge of left valve edentulous, right valve with strong and posteriorly elongate lateral teeth. Resilifer elongate, deep.

Type Locality: Off the mouth of the Rio de la Plata, 1,097 m.

Distribution: Atlantic Ocean: southwestern Atlantic: Brazil: off Campos Basin, Rio de Janeiro state (present study); Tramandaí, Albardão, Rio Grande do Sul (Figueiras & Sicardi, 1980). Uruguay: off the mouth of the Rio de la Plata (Smith, 1885; Figueiras & Sicardi, 1980); southern Brazil to Uruguay (Rios, 1994). Bathymetry: from 100 m (Figueiras & Sicardi, 1980) to 1,950 m (present study).

Material Examined: IBUFRJ 18774 (22°03'27"S, 39°45'07"W, 1,730 m), 08.V.02 [3 valves]; IBUFRJ 18776 (22°05'45"S, 39°45'55"W, 1,730 m), 09.V.02 [1 valve]; IBUFRJ 18775 (22°05'11"S, 39°42'40"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18773 (22°39'34"S, 40°08'22"W, 1,200m), 15.V.02 [2 valves]; IBUFRJ 18777 (21°52'51"S, 39°48'11"W, 1,350 m), 12.XII.02 [2 valves]; IBUFRJ 18778 (22°41'35"S, 40°00'45"W, 1,950 m), 22.XI.02 [1 valve]; IBUFRJ 18779 (22°36'03"S, 39°57'54"W, 1,650 m), 16.XI.02 [2 valves]; IBUFRJ 18780 (22°04'45"S, 39°46'31"W, 1,650 m), 27.VI.03 [1 valve]; IBUFRJ 18781 (21°52'51"S, 39°48'12"W, 1,350 m), 26.VI.03 [1 valve]; IBUFRJ 18782 (21°52'41"S, 39°46'17"W, 1,650 m), 26.VI.03 [1 valve]; IBUFRJ 18783 (21°52'43"S, 39°40'41"W, 1,950 m), 26.VI.03 [1 valve]; IBUFRJ 18784 (22°27'31"S, 40°09'23"W, 750 m), 18.VI.03 [1 valve]; IBUFRJ 18785 (22°36'12"S, 39°58'22"W, 1,650 m), 13.VI.03 [1 valve]; IBUFRJ 18786 (22°28'46"S, 39°53'27"W, 1,650 m), 17.VI.03 [1 valve]; IBUFRJ 18787 (22°30'34"S, 39°51'44"W, 1,950 m), 16.VI.03 [3 valves]; *C. platensis*: type: NHMUK 1887.2.9.2417, off the mouth of the Rio de la Plata, 1,097 m.

Discussion: The material studied here is shorter than the types (Figs. 31, 32), and the rostral ridge is of variable strength in our material and is barely visible in the type. Nevertheless, we regard this divergence as a result of the difference in size between the types and our material.

Cuspidaria fraterna is indistinguishable from *C. platensis,* except in the absence of the rostral ridge in the former. Considering that this character may be more or less developed in different specimens of *C. platensis*, we have serious doubts about retaining both species as distinct.

Rios (2009) made reference to *C. platensis*, but the figured specimen (Rios, 2009: 606, fig. 1676) does not fit in the concept of this species. *Cuspidaria plantensis sensu* Rios (2009) differs from *C. platensis* in the presence, in the former, of a somewhat triangular shell, a strongly oblique anterodorsal margin, and no posteroventral sinuation.

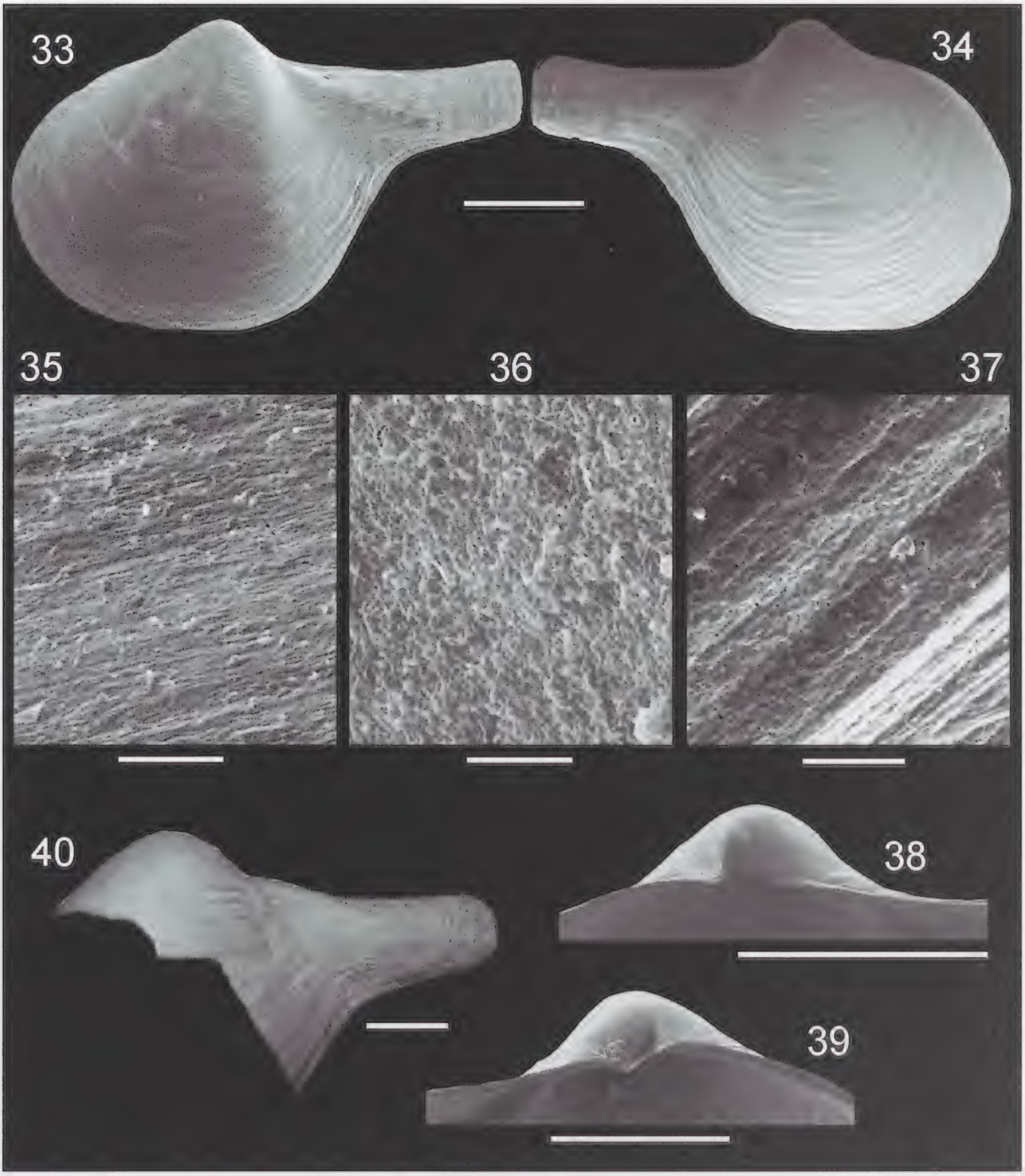
Cuspidaria wollastonii (Smith, 1885)
(Figs. 33–40)

Neaera wollastonii Smith, 1885: 40, pl. 10, fig. 6–6b.
Cuspidaria wollastonii: Dautzenberg (1889: 87; 1927: 336–337); Dautzenberg & Fischer (1897: 221); Locard (1898: 171, pl. 8, figs. 6–11); Knudsen (1970: 220); Abbott (1974: 565); Poutiers & Bernard (1995: 149, 168).

Description: Shell white, small (height, 4–5 mm; length 8–9 mm), elongate, inequivalve, inequilateral, rostrate, very convex, umbo large, central. Rostrum slender, long. Posterodorsal margin slightly curved upwards, posteroventral sinuation well marked, ventral margin moderately straight, anterior margin rounded. Externally ornamented with commarginal growth lines, rostrum with about four radial striae. Micropits absent. Hinges of both valves edentulous. Resilifer elongate, deep.

Type Locality: W of Azores, 1,829 m.

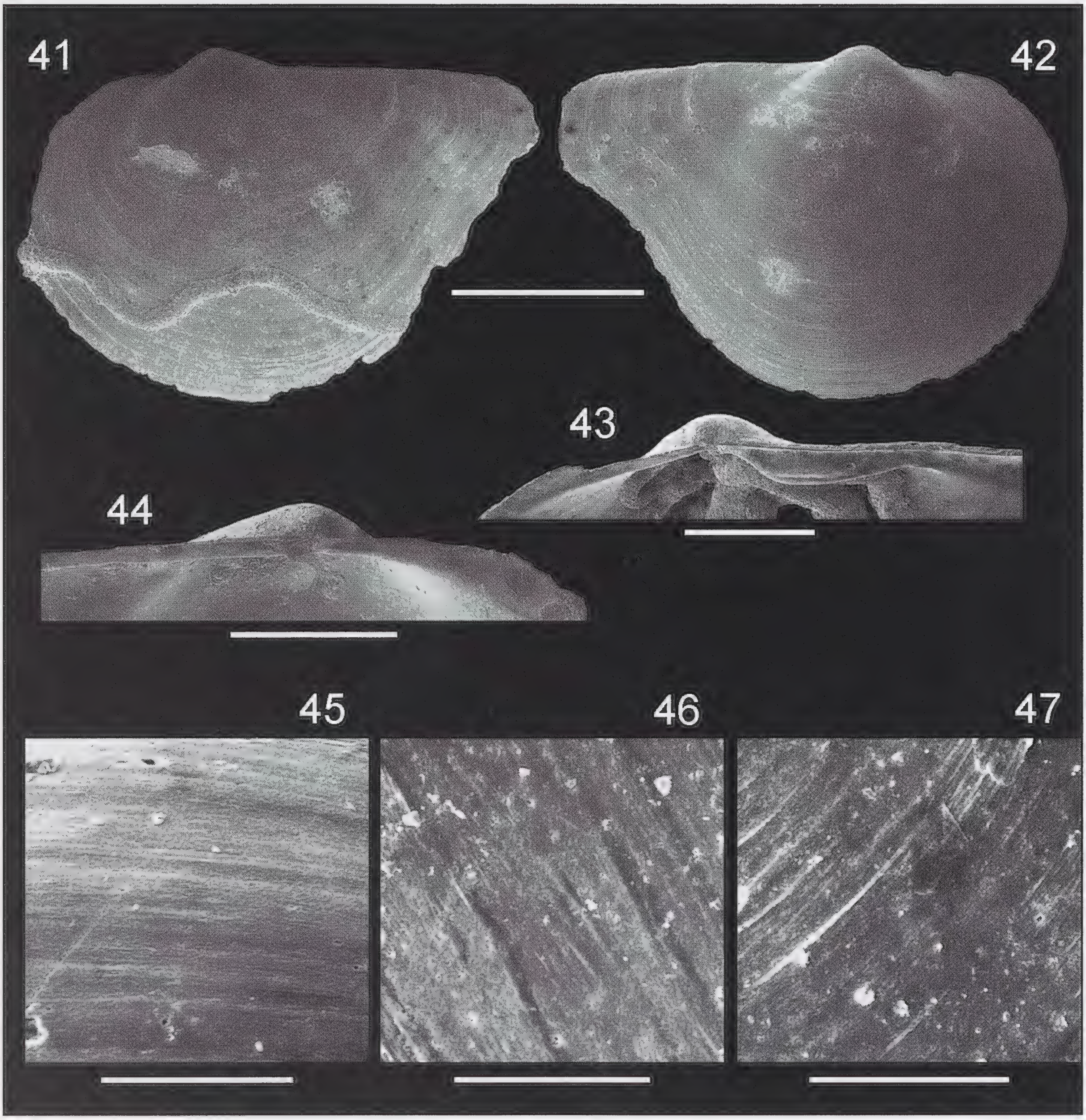
Distribution: Atlantic Ocean: southeastern Atlantic: Brazil: off Campos Basin, Rio de Janeiro state (present study); northwestern Atlantic: off Marocco, off Gulf of Cadiz (Locard, 1898), off Azores (Smith, 1885; Dautzenberg, 1889, 1927; Dautzenberg & Fischer, 1897; Locard, 1898). Bathymetry: from 103 m to 3,175 m (Locard, 1898). Abbott (1974: 565) recorded this species from "1,000 fathoms, 32 miles southwest of Bermuda", but we were unable



FIGS. 33–40. *Cuspidaria wollastonii* (Smith, 1885). FIG. 33: IBUFRJ 18806, external view, left valve; FIGS. 34–39: IBUFRJ 18807; FIG. 34: External view, right valve; FIGS. 35–37: Umbo, rostrum and anterior margin details, respectively; FIGS. 38, 39: Hinge details, right and left valve, respectively; FIG. 40: Type (NHMUK 1887.2.9.2405). Scale bars: FIGS. 33, 34, 38, 39 = 2 mm, FIGS. 35–37 = 20 µm, FIG. 40 = 4 mm.

to find this record in the literature. Knudsen (1970: 220) rejected depth records of 53 abyssal pelecypods, including the record of *C. wollastonii,* because they were based on empty shells. Up to the present, this species has been mentioned by only the five authors listed above. All of them recorded *C. wollastonii* for deep water, except Locard (1898) who recorded it from 103 to 3,175 m. Considering that there is no record of *C. wollastonii* with soft parts from shallow waters and only one of five reports recorded this species outside the deep-water environment, we cannot reject the deep-water records.

Material Examined: IBUFRJ 18806 (22°06'52"S, 39°44'13"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18807 (22°06'52"S, 39°44'13"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18808 (22°04'45"S, 39°46'31"W, 1,650 m), 27.VI.03



FIGS. 41–47. *Cuspidaria* cf. *barnardi* Knudsen, 1970, IBUFRJ 18804. FIG. 41: External view, left valve; FIG. 42: External view, right valve; FIGS. 43, 44: Hinge details, right and left valve, respectively; FIGS. 45–47: Umbo, rostrum and anterior margin details, respectively. Scale bars: FIGS. 41, 42 = 2 mm, FIGS. 43, 44 = 1 mm, FIGS. 45–47 = 100 µm.

[1 valve]; IBUFRJ 18809 (22°41’10”S, 40°02’20”W, 1,650 m), 13.VI.03 [1 valve]; *C. wollastonii*: type: NHMUK 1887.2.9.2405, W of Azores, 1,829 m.

Discussion: This type is broken but not destroyed (Fig. 40). The figure provided by Smith (1885, pl. 10, fig. 6–6b) is somewhat different from the type, because the rostrum is more elongate in Smith’s figure. Considering that the type is composed of only one valve, we suppose that this difference can be attributed to the drawing.

Cuspidaria wollastonii is similar to *C. rostrata*, but it differs by the presence, in the former, of a more inflated shell, a shorter rostrum, and a somewhat quadrangular outline; whereas *C. rostrata* is more circular in outline and has a very long and slender rostrum.

The specimen illustrated by Salas (1996: 74, figs. 111, 112) under the name *C. wollastonii* does not fit in the concept of *C. wollastonii*. This specimen may eventually prove to be an extreme variation of *C. rostrata,* or even a new taxon.

Cuspidaria cf. *barnardi* Knudsen, 1970
(Figs. 41–47)

Cuspidaria barnardi Knudsen, 1970: 139–141, figs. 96, 97; Poutiers (1984: 287, pl. 17, fig. 4); Allen & Morgan (1981: 457–458, fig. 24); Poutiers & Bernard (1995: 148, 157); Scarabino (2003: 238); Allen (2008: 79, 95, 117, 161).

Description: Shell white, small (height, 4 mm; length, 5 mm), elongate, inequivalve, inequilateral, rostrate, little convex. Umbo small, central. Rostrum short. Dorsal margin straight, posteroventral sinuation little pronounced, ventral margin and anterior margin rounded. Externally ornamentated only by commarginal growth lines. Micropits absent. Hinge of left valve edentulous, right valve with strong posterior teeth. Resilifer rounded, shallow.

Type Locality: Indian Ocean: off southeast Africa, 3,530 m

Distribution: Indian Ocean: off SE Africa (Knudsen, 1970), SE of Glorioso Islands (Poutiers, 1984). Atlantic Ocean?: North Atlantic: S of Martha’s Vineyard, W of Guinea-Bissau (Allen & Morgan, 1981). Southwestern Atlantic: off Campos Basin, Rio de Janeiro state (present study); off Uruguay (Allen & Morgan, 1981). Bathymetry: from 1,050 m (present study) to 3,828 m (Allen & Morgan, 1981).

Material Examined: IBUFRJ 18804 (22°04’33”S, 39°52’05”W, 1,050 m), 30.VI.03 [2 valves].

Discussion: The specimens collected in the present study show good agreement with the original concept of *C. barnardi* (Knudsen, 1970: 139–141, figs. 96, 97). The major difference between our material and the illustration of the type is the posterodorsal margin that is somewhat curved and slightly descending in our specimens, whereas the original illustration shows it as straight and horizontal. However, this difference may be a result of an old injury in our specimens, as noted by the shell scar in that region.

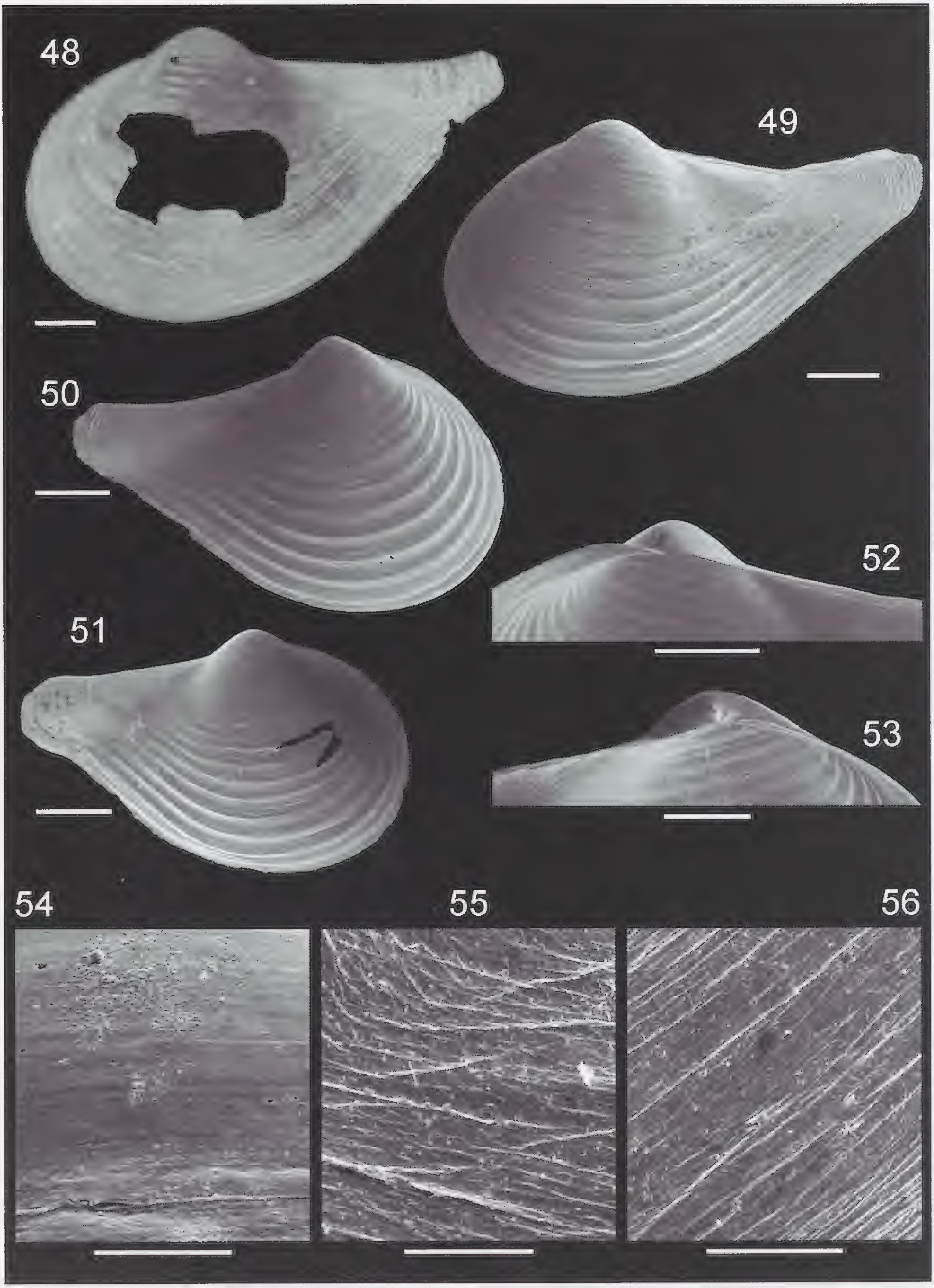
Nevertheless, despite their conchological similarity, considering that the type locality of *C. barnardi* is the Indian Ocean, we have identified this taxon with some uncertainty. Because there is as yet no convincing evidence about the geographic distribution of deep-sea septibranch species, we opted at this time to retain taxa from different oceans as potentially different species (Oliveira & Absalão, 2010).

Cuspidaria papyria Jeffreys, 1876
(Figs. 48–56)

Neaera papyria Jeffreys, 1876: 498.
Cuspidaria? *papyria*: Poutiers & Bernard (1995: 164).

Redescription: Shell white, small (height, 2.0–4.5 mm; length, 4–8 mm), elongate, inequivalve, inequilateral, rostrate, convex. Umbo large, prosogyrous. Rostrum large, long. Posterodorsal margin curved upwards, posteroventral margin gently merging with ventral margin, posteroventral sinuation absent, anterior margin rounded, anterodorsal margin curved downwards immediately after the umbo. Shell with about 6–18 commarginal waves, internally perceptible. Externally ornamented with indistinct commarginal growth lines, several radial lines extending over the rostrum. Micropits absent. Hinge edentulous, small triangular process often present. Resilífer triangular, elongate, shallow.

Type Locality: “Valorous” Expedition, sta. 12, SE of Greenland (56°11’N, 37°41’W, 2,652 m).



FIGS. 48–56. *Cuspidaria papyria* Jeffreys, 1876. FIG. 48: Lectotype, USNM 63958, external view, left valve; FIG. 49: MNHN, external view, left valve; FIG. 50: MCZ 374245, external view, right valve; FIG. 51: MZSP 96913, external view, right valve; FIGS. 52, 53: Hinge details, right (MOFURG 51167) and left (MNRJ 18730) valves, respectively; FIGS. 54–56: IBUFRJ 18872, umbo, rostrum and anterior margin details, respectively. Scale bars: FIGS. 48–53 = 1 mm, FIGS. 54–56 = 100 μm.

Distribution: Atlantic Ocean: Northwest Atlantic: SE of Greenland (Jeffreys, 1876). Southwest Atlantic: Brazil: off Campos Basin, Rio de Janeiro state (present study). Bathymetry: from 1,050 m (present study) to 2,652 m (Jeffreys, 1876).

Material Examined: IBUFRJ 18871 (21°58'36"S, 39°46'30"W, 1,700 m), 08.X.01 [2 valves]; IBUFRJ 18872 (22°05'11"S, 39°42'40"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18876 (22°04'46"S, 39°43'02"W, 1,950 m), 24.XI.02 [1 valve]; IBUFRJ 18877 (21°52'41"S, 39°46'17"W, 1,650 m), 11.XII.02 [2 valves]; IBUFRJ 18878 (21°52'44"S, 39°40'45"W, 1,950 m), 11.XII.02 [1 valve]; IBUFRJ 18879 (22°41'03"S, 40°02'29"W, 1,650 m), 23.XI.02 [1 spec.]; IBUFRJ 18880 (22°41'35"S, 40°00'45"W, 1,950 m), 22.XI.02 [2 valves]; IBUFRJ 18881 (22°31'28"S, 40°03'50"W, 1,050 m), 19.XI.02 [1 valve]; IBUFRJ 18882 (22°36'03"S, 39°57'54"W, 1,650 m), 16.XI.02 [2 valves]; IBUFRJ 18883 (22°28'49"S, 39°53'24"W, 1,650 m), 17.XI.02 [1 spec.]; IBUFRJ 18884 (22°33'10"S, 39°54'22"W, 1,950 m), 23.XI.02, [1 spec.]; IBUFRJ 18885 (22°11'16"S, 39°43'44"W, 1,950 m), 22.VI.03 [1 valve]; IBUFRJ 18886 (22°04'45"S, 39°41'58"W, 1,950 m), 27.VI.03 [3 valves]; IBUFRJ 18888 (22°41'31"S, 40°00'47"W, 1,950 m), 06.XII.03 [1 valve + 1 spec.]; IBUFRJ 18889 (22°31'28"S, 40°03'49"W, 1,050 m), 18.VI.03 [2 valves]; IBUFRJ 18890 (22°36'12"S, 39°58'22"W, 1,650 m), 13.VI.03 [1 valve]; IBUFRJ 18891 (22°28'46"S, 39°53'27"W, 1,650 m), 17.VI.03 [3 valves]; MNRJ 18730 (22°06'52"S, 39°44'13"W, 1,930 m), 08.V.02 [1 valve]; MZSP 96913 (22°48'05"S, 40°06'38"W, 1,950 m), 06.XII.03 [1 valve]; MOFURG 51167 (22°06'52"S, 39°44'13"W, 1,930 m), 08.V.02 [1 valve]; MCZ 374245 (22°48'05"S, 40°06'38"W, 1,950 m) 06.XII.03 [1 valve]; MNHN (22°05'11"S, 39°42'40"W, 1,930 m), 08.V.02 [1 valve].

Discussion: *Cuspidaria papyria* was poorly described and never figured. We have been able to examine the type series (USNM 63958), which is composed of several fragments and one broken valve (Fig. 48). The broken valve is very similar to our specimens and an appropriate description is given here.

Cuspidaria papyria has a distinct rippled appearence observed in only a very few species of *Cuspidaria*. It can be distinguished from *C. tenella* in the absence of conspicuous commarginal striae, and by the elongate outline, with a longer rostrum in the former. It is noteworthy that, although the type specimen of *C. tenella* is broken (Zelaya & Ituarte 2006, fig. 29), the concept of *C. tenella* established by Dell (1990: 60, fig. 105) perfectly agrees with the fragmented type specimen and fits the original concept of this species.

Additionally, although Dell (1964, 1990) synonymized *C. tenella* and *C. plicata*, we consider them as distinct species because they differ in several diagnostic features for the cuspidariids: (1) The anterodorsal margin of *C. tenella* is descending, gently merging with the anterior margin, whereas in *C. plicata* the anterodorsal margin forms a strong shoulder; (2) The posterodorsal margin is strongly oblique in *C. tenella*, but in *C. plicata* it is almost parallel to the anterodorsal axis; (3) The posteroventral sinuation is less developed in *C. tenella* than in *C. plicata*; (4) The external ornamentation of *C. tenella* has conspicuous commarginal striae, which are barely visible in *C. plicata*, which in turn has commarginal waves not seen in *C. tenella*.

Cuspidaria papyria can also be distinguished from *C. plicata* in the presence, in the former species, of a large and elongate rostrum, posteroventral sinuation absent, and a barely perceptible shoulder; *C. plicata* has a shorter rostrum, a marked posteroventral sinuation, a long anterodorsal shoulder, and fewer and more widely spaced waves. In addition, *C. papyria*. has a distinctly elongate outline, and the umbo is closer to the anterior margin, whereas *C. plicata* is more rounded, with a central umbo.

***Cuspidaria tamandua* n. sp.**

(Figs. 57–63)

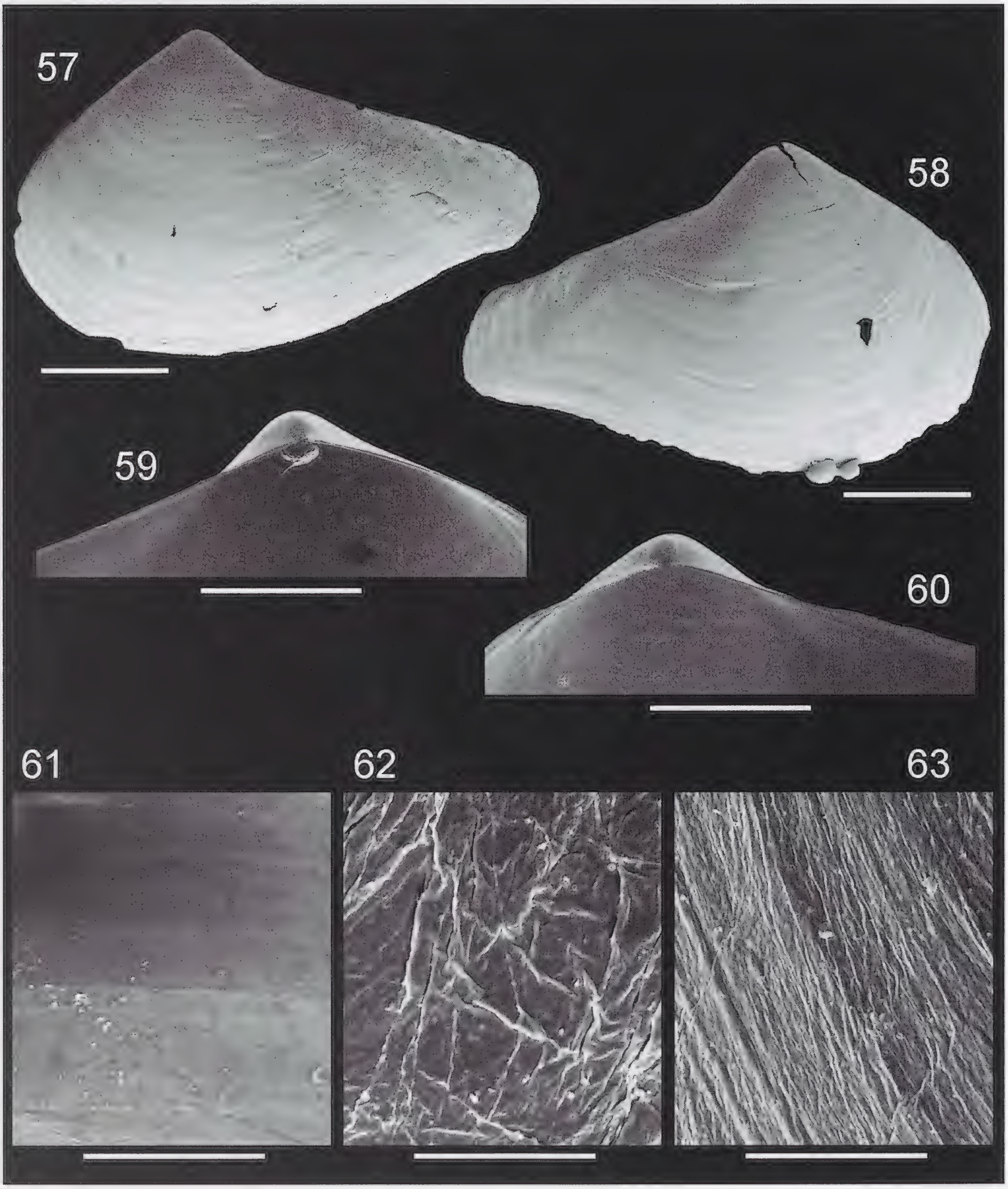
Description: Shell white, small (height, 1–3 mm; length, 2–5 mm), elongate, inequivalve, inequilateral, rostrate, slightly convex. Umbo triangular, projecting. Rostrum large, long. Posterodorsal margin straight, descending, posteroventral margin weakly sinuate, gently merging with ventral margin, anterior margin rounded, anterodorsal margin almost straight, descending. Externally ornamented with indistinct commarginal growth lines, few radial striae present on rostrum. Micropits absent. Hinge edentulous. Resilifer not apparent.

Etymology: This species is named for its shape, which resembles the skull of myrmecophagids (Mammalia: Xenarthra), anteaters from Central and South America. The word "tamanduá" was incorporated into the Portuguese language from Tupi, the native language of most Brazilian indigenous peoples. The name is employed as a noun in apposition.

Type Locality: off Campos Basin, Rio de Janeiro state, Brazil. Depth: 1950 m.

Distribution: Only known from type locality. Bathymetry: from 1,050 m to 1,950 m.

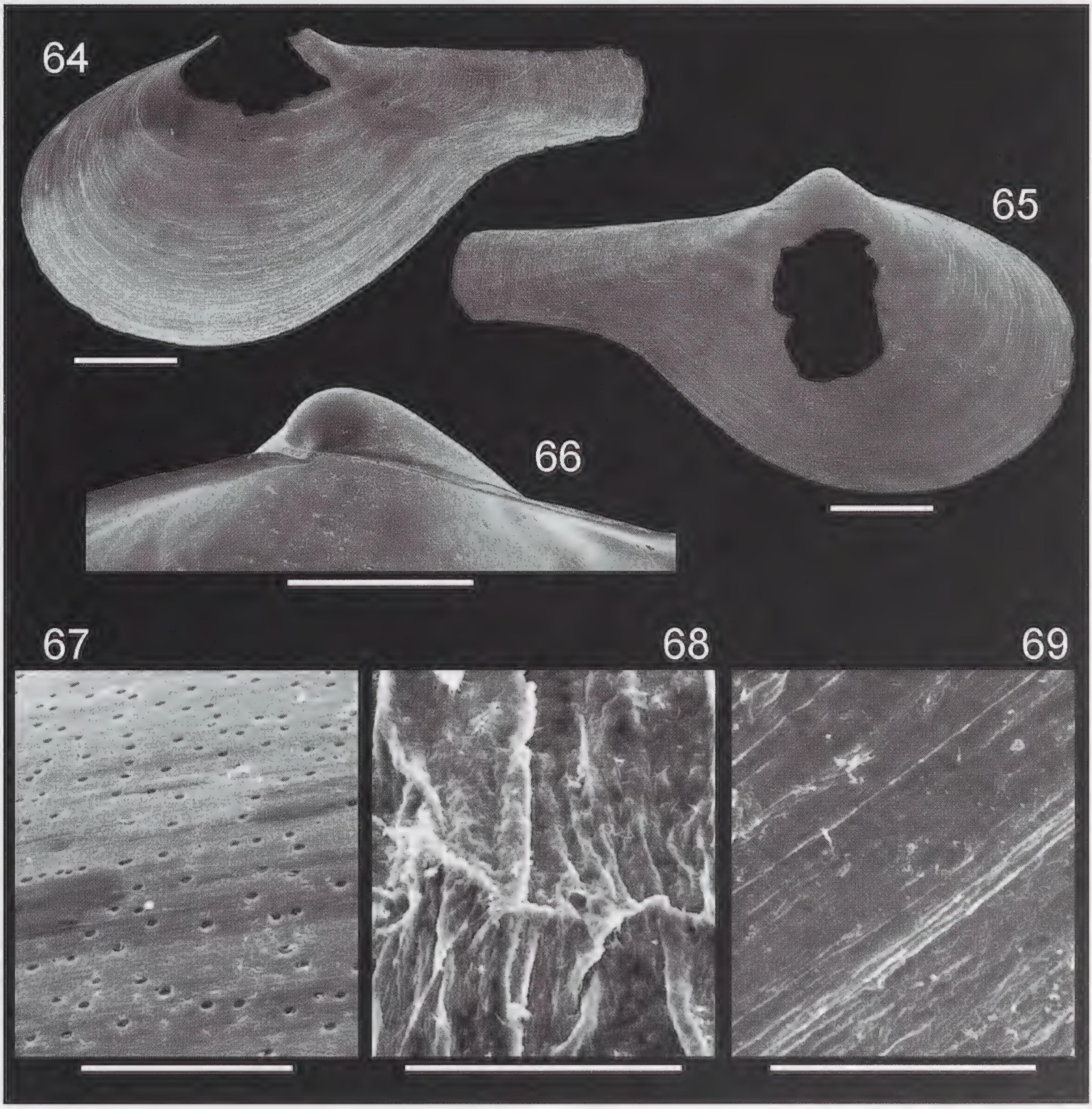
Type Material: Holotype, IBUFRJ 18790 (22°11'04"S, 39°47'04"W, 1,650 m), 25.XI.02 [1 valve]; Paratypes: IBUFRJ 18791 (22°11'16"S,



FIGS. 57–63. ***Cuspidaria tamandua*** n. sp. FIG. 57: Holotype, IBUFRJ 18790, external view, left valve; FIG. 58: Paratype, MCZ 374244, external view, right valve; FIGS. 59, 60: Paratypes, hinge details, left (MOFURG 51171) and right (IBUFRJ 18791) valves, respectively; FIGS. 61–63: Paratype, MNRJ 18729, umbo, rostrum and anterior margin details, respectively. Scale bars: FIGS. 57–60 = 1 mm, FIGS. 61–63 = 100 µm.

39°43'44"W, 1,950 m), 25.XI.02 [1 valve]; MNRJ 18729 (22°31'37"S, 39°55'14"W, 1,650 m), 16.VI.03 [1 valve]; MZSP 96912 (22°37'02"S, 39°56'20"W, 1,950 m), 13.VI.03 [2 valves]; MOFURG 51171 (22°05'11"S, 39°42'40"W, 1,930 m), 08.V.02 [2 valves]; MCZ 374244 (22°04'45"S, 39°41'58"W, 1,950 m), 27.VI.03 [1 valve]; MNHN (22°31'37"S, 39°55'14"W, 1,650 m), 16.VI.03 [1 valve].

Material Examined: IBUFRJ 18788 (22°09'10"S, 39°44'50"W, 1,930 m), 08.V.02 [1 valve]; IBUFRJ 18792 (22°11'16"S, 39°43'44"W, 1,950 m), 25.XI.02 [2 valves]; IBUFRJ 18793 (22°31'28"S, 40°03'50"W, 1,050 m), 19.XI.02, [1 valve]; IBUFRJ 18794 (22°36'03"S, 39°57'54"W, 1,650 m), 16.XI.02, [6 valves]; IBUFRJ 18795 (22°33'10"S, 39°54'22"W, 1,950 m), 23.XI.02 [4 valves]; IBUFRJ 18796 (22°11'16"S, 39°43'44"W, 1,950 m), 22.VI.03 [1 valve]; IBUFRJ 18798 (21°57'26"S, 39°40'34"W, 1,950 m), 27.VI.03 [1 valve]; IBUFRJ 18799 (21°57'26"S, 39°40'34"W, 1,950 m), 27.VI.03 [3 valves]; IBUFRJ 18800 (21°57'26"S,



FIGS. 64–69. ***Cuspidaria wapixana*** n. sp., holotype, IBUFRJ 18805. FIG. 64: External view, left valve; FIG. 65: External view, right valve; FIG. 66: Hinge details, right valve; FIGS. 67–69: Umbo, rostrum and anterior margin details, respectively. Scale bars: FIGS. 64, 65 = 1 mm, FIG. 66 = 500 μm, FIGS. 67–69 = 50 μm.

39°40'34"W, 1,950 m), 27.VI.03 [3 valves]; IBUFRJ 18801 (21°52'43"S, 39°40'41"W, 1,950 m), 26.VI.03 [2 valves]; IBUFRJ 18802 (22°31'28"S, 40°03'49"W, 1,050 m), 18.VI.03 [4 valves]; IBUFRJ 18803 (22°30'34"S, 39°51'44"W, 1,950 m), 16.VI.03 [2 valves].

Discussion: ***Cuspidaria tamandua*** n. sp. differs from all previously known species recorded for Brazil in its edentulous hinge, weakly marked posteroventral sinuation, large rostrum, and faintly visible external ornamentation.

The most similar species to ***Cuspidaria tamandua*** n. sp. is *C. sulcifera*. However, ***C. tamandua*** n. sp. has a projecting triangular umbo, a descending posterodorsal margin, absence of both an axial ridge and a deep furrow between the rostrum and the disk of the shell, and a simple hinge without a tooth or condrophore, whereas *C. sulcifera* has a blunte umbo, a horizontally oriented posterodorsal margin that is usually slightly pointed upwards, an axial ridge before a deep furrow between the rostrum and the disk of the shell, and an oblique chondrophore on the left valve.

Cuspidaria luymesi (see Knudsen, 2005: 126–128, fig.3) is also somewhat similar to ***C. tamandua*** n. sp., but differs in the presence, in the former species, of a horizontally oriented posterodorsal margin, a more elongate rostrum, and a long posterior lateral tooth on the right valve.

Cuspidaria wapixana n. sp.

(Figs. 64–69)

Description: Shell white, small (height, 3.1 mm; length, 6.2 mm), elongate, inequivalve, inequilateral, rostrate, convex, umbo triangular, central. Rostrum slender, very long. Posterodorsal margin straight, posteroventral sinuation well marked, ventral margin gently curved, anterior margin rounded, extended, anterodorsal margin slightly oblique. Externally ornamented by commarginal growth lines, rostrum with about four radial striae. Micropits present only on interdissoconch. Hinge edentulous. Resilifer not apparent.

Etymology: This species is dedicated to the Wapixana Native American people, who live in northern Brazil in the Amazon Forest. The name is employed as a noun in apposition.

Type Locality: off Campos Basin, Rio de Janeiro state, Brazil. Depth: 1,930 m.

Distribution: Only known from type locality. Bathymetry: 1,930 m.

Material Examined: Type Material: Holotype, IBUFRJ 18805 (22°09'10"S, 39°44'50"W, 1,930 m), 08.V.02 [2 valves].

Discussion: Unfortunately this species is very fragile and rare, and one of the two valves was damaged during process of taking the SEM photographs.

Cuspidaria wapixana n. sp. differs from ***C. tamandua*** n. sp. in the presence, in ***C. wapixana*** n. sp., of a strongly elongate outline and a long, slender rostrum.

Cuspidaria wapixana n. sp. differs from previously known species recorded for Brazil but it has the same general features observed for *C. rostrata* and *C. wollastonii*. However, ***C. wapixana*** n. sp. differs from both species because: (1) *Cuspidaria rostrata* has a less extended anterior margin and a longer and more slender rostrum; (2) *Cuspidaria wollastonii* has a strong posteroventral sinuation and an inflated shell.

ACKNOWLEDGMENTS

Our thanks are to Dr. Elena M. Krylova (from P. P. Shirshov Institute of Oceanology) and Dr. Alexander Sysoev (from Zoological Museum of Moscow State University) for the loan of the type material deposited at Zoological Museum of Moscow, to Dr. Michèle Bruni and Dr. Michel Dagnino (both from Oceanographic Museum of Monaco) for the photo of the type of *C. munieri*, to Dr. Ellen Strong and Yolanda Villacampa (both from Smithsonian National Museum of Natural History) for the photo of the type of *C. circinata*, to PETROBRAS (Brazilian Petroleum Co.) for making this material available and for SEM support. This research was partially supported by fellowships from CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico).

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Revised ms. accepted 28 February 2011

MALACOLOGIA, 2011, 54(1–2): 139–146

EFFECTS OF DIFFERENT CALCIUM CONCENTRATIONS SUPPLEMENTED ON THE DIET OF *PARTULA GIBBA* ON THEIR MORPHOMETRIC GROWTH PARAMETERS, WEIGHT AND REPRODUCTION SUCCESS

Ana R. Gouveia[3*], Paul Pearce-Kelly[1], Donald L. J. Quicke[2] & Simon R. Leather[3]

ABSTRACT

Partula gibba, commonly known as the Fat Guam *Partula*, is endemic to Guam and Northern Mariana Islands, and it is listed as endangered in the IUCN Red List of Threatened Species. The effects of calcium concentration on its growth and reproductive success were studied.

The snails were divided into six groups, fed *ad libitum* on a diet based on the one formulated by Frame and Clarke at the Nottingham University approximately 25 years ago or variants in which cuttlebone was substituted by various concentrations of calcium carbonate. Shell height, thickness and width, aperture/lip height and width where recorded every month for a whole year, and all were found to be significantly positively correlated with the percentage of added calcium carbonate in the diet (range 0–40% dry wt:wt). Morphometric growth parameters of snails fed 20% added calcium carbonate did not differ significantly from the diet with added cuttlebone (20%), with the exception of their reproductive success, which was lower with the cuttlebone treatment. Reproduction success (expressed by the number of newborns per adult per month) was also significantly and positively correlated over the range of added calcium carbonate to the diet.

Key words: *Partula* snails, calcium, growth parameters, reproductive success, diet.

INTRODUCTION

Partula gibba, commonly known as the Fat Guam *Partula*, is endemic to Guam and the Northern Mariana Islands, and is listed as endangered in the IUCN Red List of Threatened Species.

Gastropod distributions may depend on various factors, but calcium concentration has been found to be a particularly important and limiting (Brodersen & Madsen, 2003). The importance of calcium to terrestrial gastropods is well known, and the observations are almost always similar to the early description of Boycott (1934), who showed that dietary calcium is essential for growth, reproduction and shell construction (Wagge, 1952; Crowell, 1973; Ireland, 1991; Ireland & Marigomez, 1992; Egonmwan, 2008). The snails' shell comprises approximately 97% calcium carbonate and this accounts for their highly demand for this element (Heller & Magaritz, 1983).

Several studies have examined the effects of calcium concentration on various snail species (Brodersen & Madsen, 2003; Harrison, 1970; Madsen, 1987), and these have mostly concluded that the snails are generally able to live under low calcium concentrations in the laboratory, but that growth is inhibited and thinner shells are usually developed (Brodersen & Madsen, 2003). Crowell (1973) demonstrated that plant matter alone is not a sufficient source of calcium, and observed that the shells of snails fed only on plant matter were weak, thin and fragile. He also showed experimentally that *Helix aspersa* ingested soil, and that the soil subsequently passed as faeces contained 12–32% less calcium than soil with no previous exposure to snails (Heller & Magaritz, 1983), and therefore soil is likely to be an important source of calcium in the wild.

The diet of *Partula* snails in the wild is largely unknown. They are detritivores, but have been observed feeding on various plants includ-

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[1] Zoological Society of London, Outer Circle, Regent's Park, London NW1 4RY, U.K.

[2] Division of Biology, Imperial College London, Silwood Park, Ascot, Berkshire, SL5 7PY, UK, and Department of Entomology, Natural History Museum, London, SW7 5BD, U.K.

[3] Department of Biology, Imperial College London, Silwood Park, Ascot, Berkshire, UK, SL5 7PY, and the Zoological Society of London, U.K.

*Corresponding author: a.gouveia07@imperial.ac.uk

ing decaying stalks of *Hibiscus* (Malvaceae), *Etlingera* (Zingiberaceae), *Piper* (Piperaceae), *Microsorum* (Polypodiaceae), and *Cocos* (Arecaceae) (Hopper & Smith, 1992; Cunningham et al.,1996; Coote, 2007).

Partula are ovoviviparous hermaphrodites (Clarke & Murray, 1969), and they produce a completely shelled offspring every six to eight weeks.

In order to test whether calcium plays an important role in the wellbeing of the *Partula* snail cultures, we investigated the effect of different dietary mixes varying in their calcium carbonate content.

METHODS

The snails *Partula gibba* used in the experiment were the offspring from the parents from London Zoo population. Individuals were maintained in a controlled temperature room (range of 22°C at night and 23°C during the day). Relative humidity varied between 70 and 80%. Light was provided by fluorescent tubes on a twelve hour day and night cycle.

Because of the high mortality experienced during the first post natal week, *Partula gibba* were used after they reached a minimum weight of 0.03 grams and a maximum of 0.05 grams, the snails were then randomly placed into individual plastic containers (250 ml) covered with cling film®, the substratum consisted of layers of damp bleach-free paper tissue.

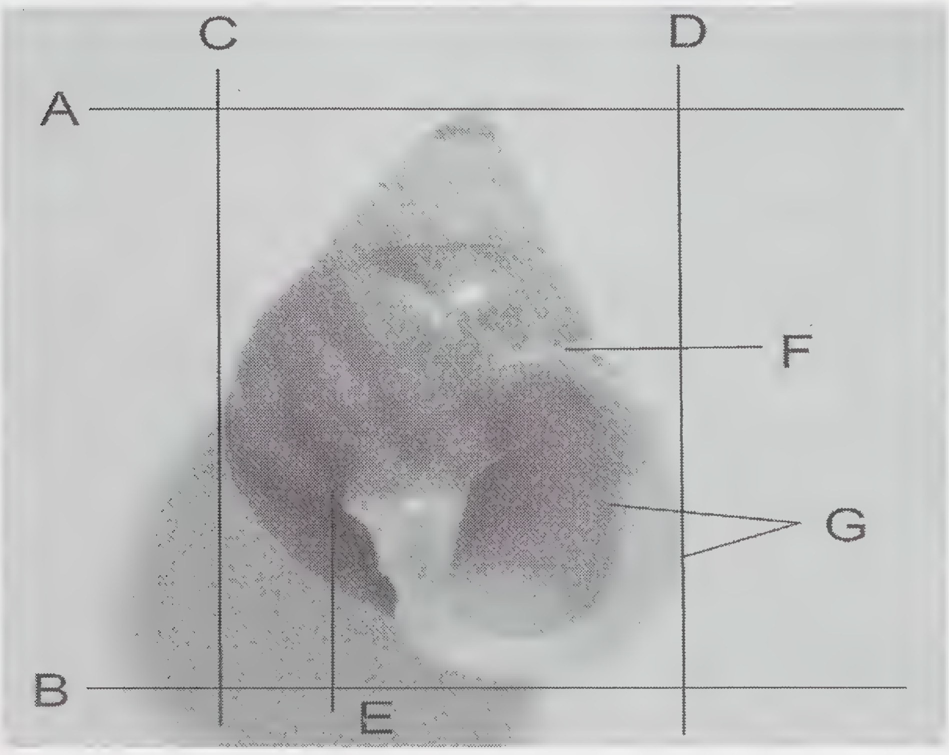

FIG. 1. Snails' morphometric measurements; shell thickness (G), height (A–B), width (C–D), lip height (B–F) and lip width (E–D).

Snails were fed *ad libitum* on a diet based on the one formulated by Frame and Clarke at the Nottingham University approximately 25 years ago (Tonge & Bloxam, 1990), 300 g of porridge oats, 150 g of powdered trout pellets, 600 g powdered grass pellets, 25 g of vitamin powder (Vetzyme, Seven Seas Ltd.) and 300 g of powdered cuttlebone. The diet was moistened with filtered water to form a runny paste and then microwaved for approximately two minutes for sterilisation.

Different groups of snails were fed either standard diet or variants in which the cuttlebone was replaced by powdered calcium carbonate 0, 10, 20, 30 and 40% (wt:wt)(Mineral Technologies, Inc.). There were 10 replicates of each treatment. The diet, tissue and the containers were replaced every month, and the numbers of newborns (reproduction success) were counted. All the materials used to handle, feed, house and clean the snails were previously sterilised/disinfected in a microwave or with water sterilized with Milton tablets (sodium hypochlorite) (Coates, 1996).

Snails were weighed once per month from the beginning of the experiment until the end. Due to their thin delicate shells, morphometric measurements were only conducted once the snails reached the adults stage (characterized by the formation of the lip (P. Pearce-Kelly, personal observation)). Shell height, thickness and width, aperture/lip height and width of each snail were measured using a digital vernier calliper, based on the pathology protocol in use at the Zoological Society of London, Pathology Department (Fig. 1). The snails' measurements were recorded once per month for a whole year.

Statistical analyses of the data were performed using the software package R (Ihaka & Gentleman, 1996).

RESULTS

Results for changes in morphometric parameter between each monthly measurement are showed in Figs. 2–8. All morphological measures as well as snail weight were found to be significantly and positively correlated with the percentage of added calcium carbonate in the diet (Table 1.).

In addition, reproductive success (expressed by the number of newborns per adult per month) was significantly and positively correlated over the range of added calcium carbon-

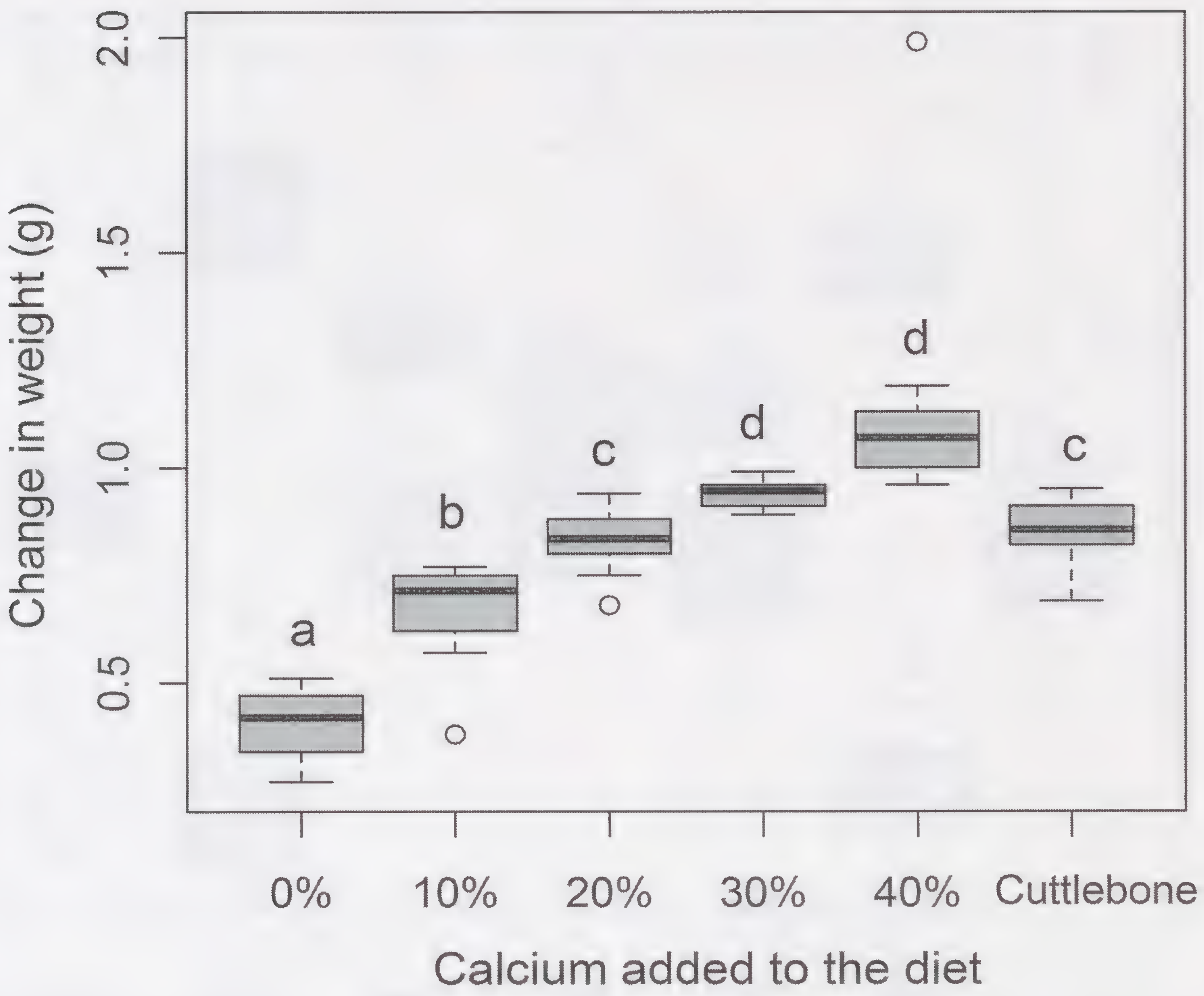

FIG. 2. Effects of different calcium carbonate concentrations added to the diet including 20% powdered cuttlebone on the weight of the snails. The top and bottom of each rectangular box denote the 75th and 25th percentiles, respectively, with the median shown inside the box. Horizontal bars on lines extending from each box represent the 90th and 10th percentiles, and the outliers are illustrated as "o". Significant differences among individual treatments are denoted with letters over each box. (Statistics are presented in the same format for all of the box plots in this study).

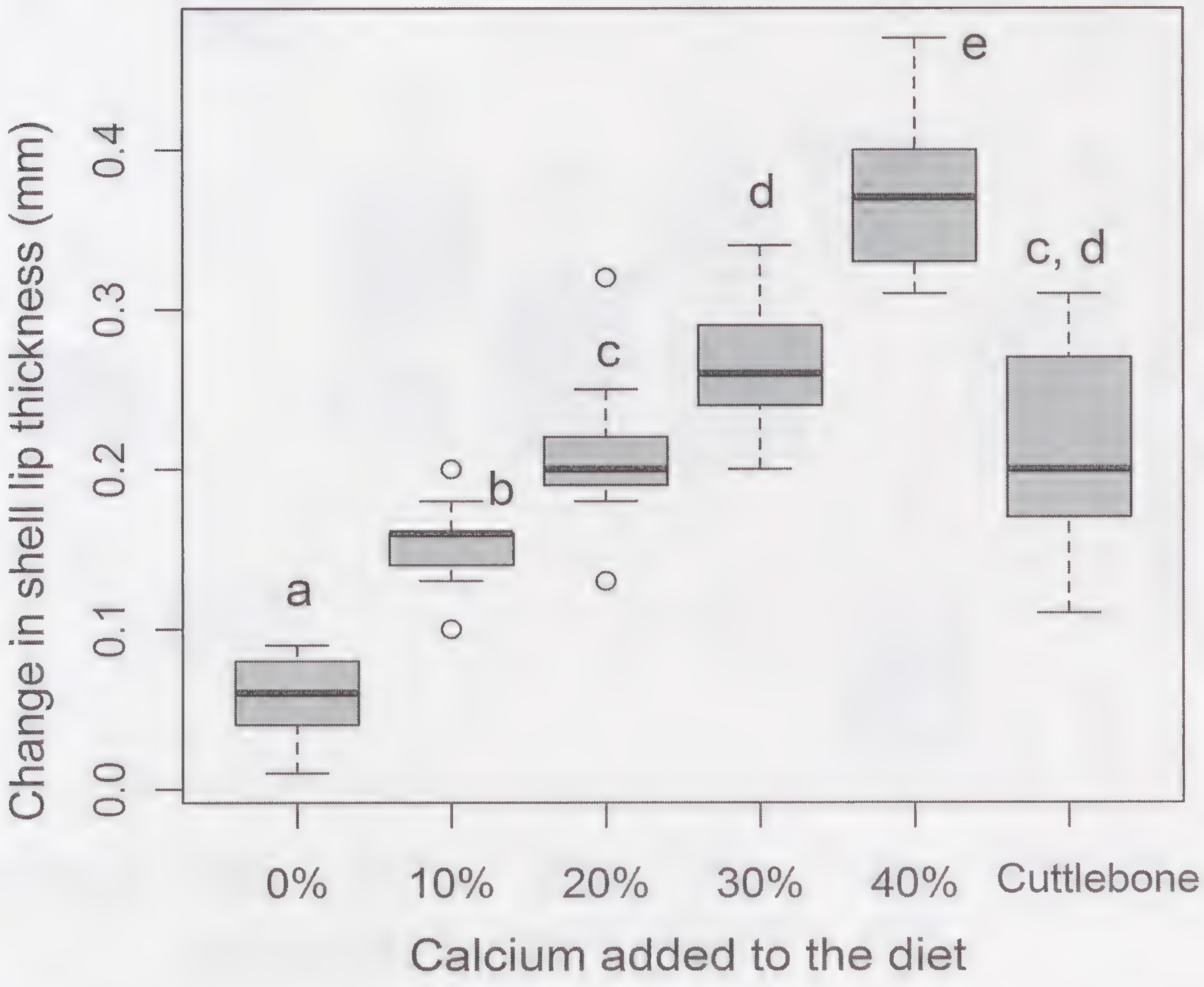

FIG. 3. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the snails' shell lip thickness.

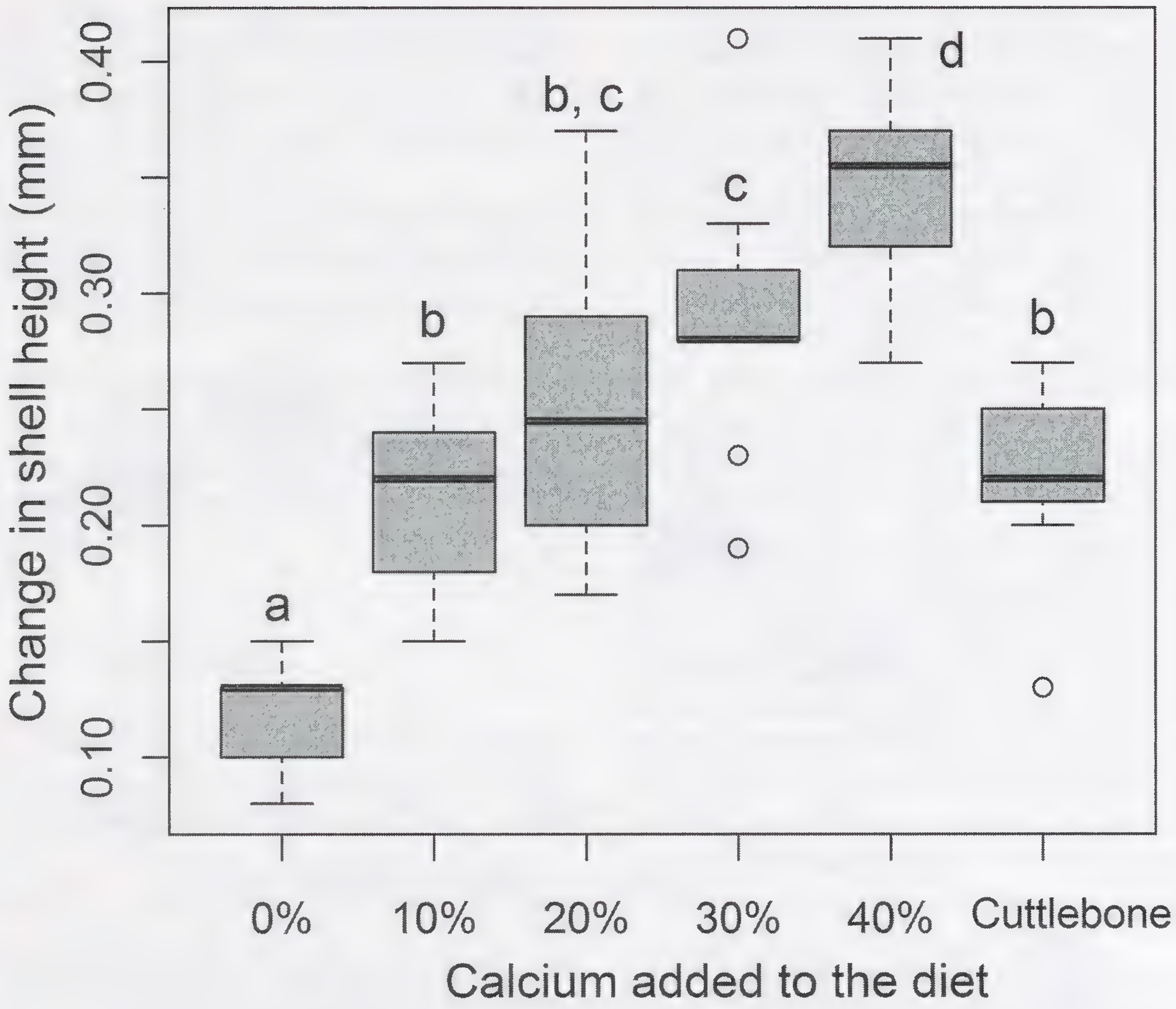

FIG. 4. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the snails' shell height.

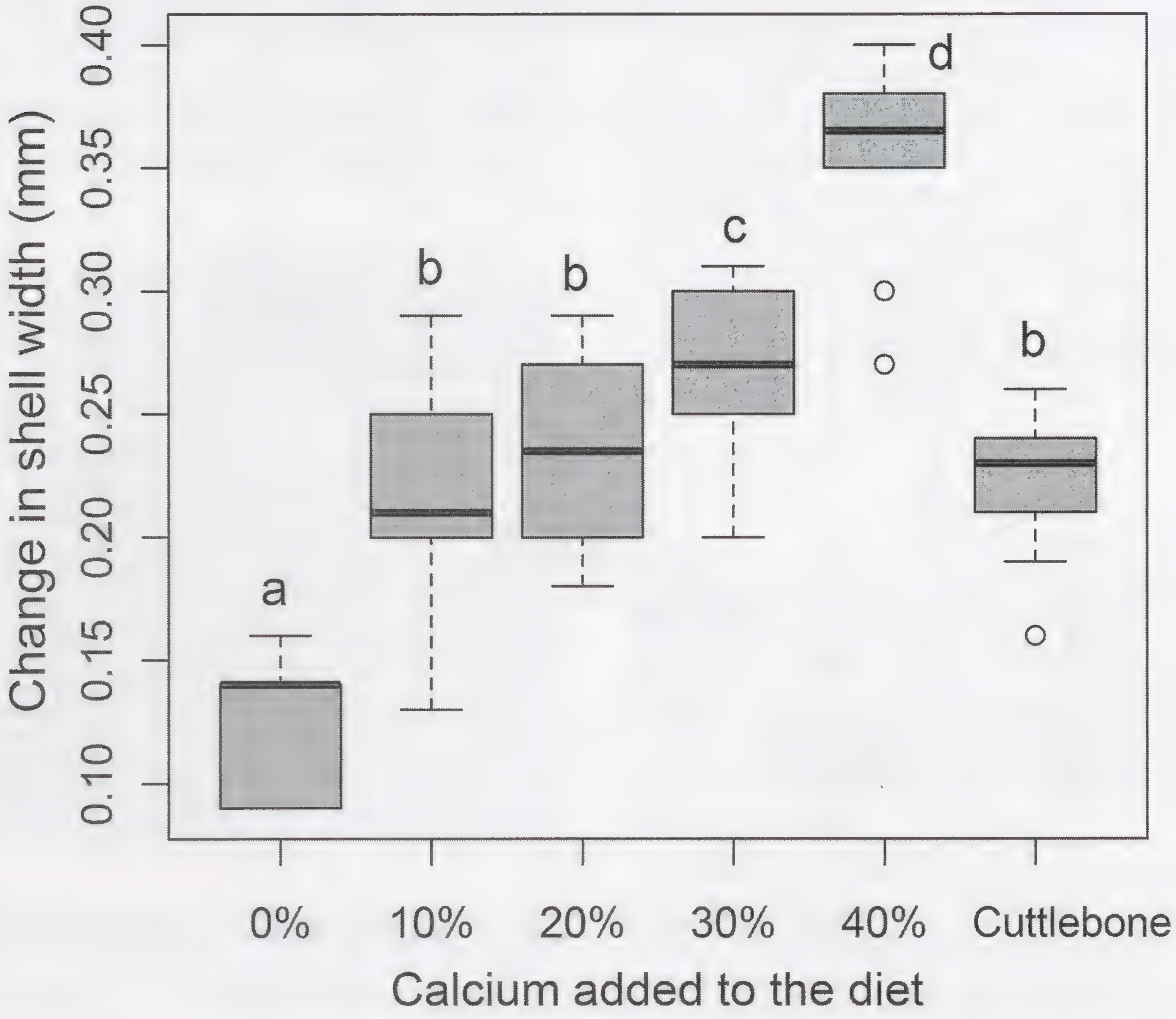

FIG. 5. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the snails' shell width.

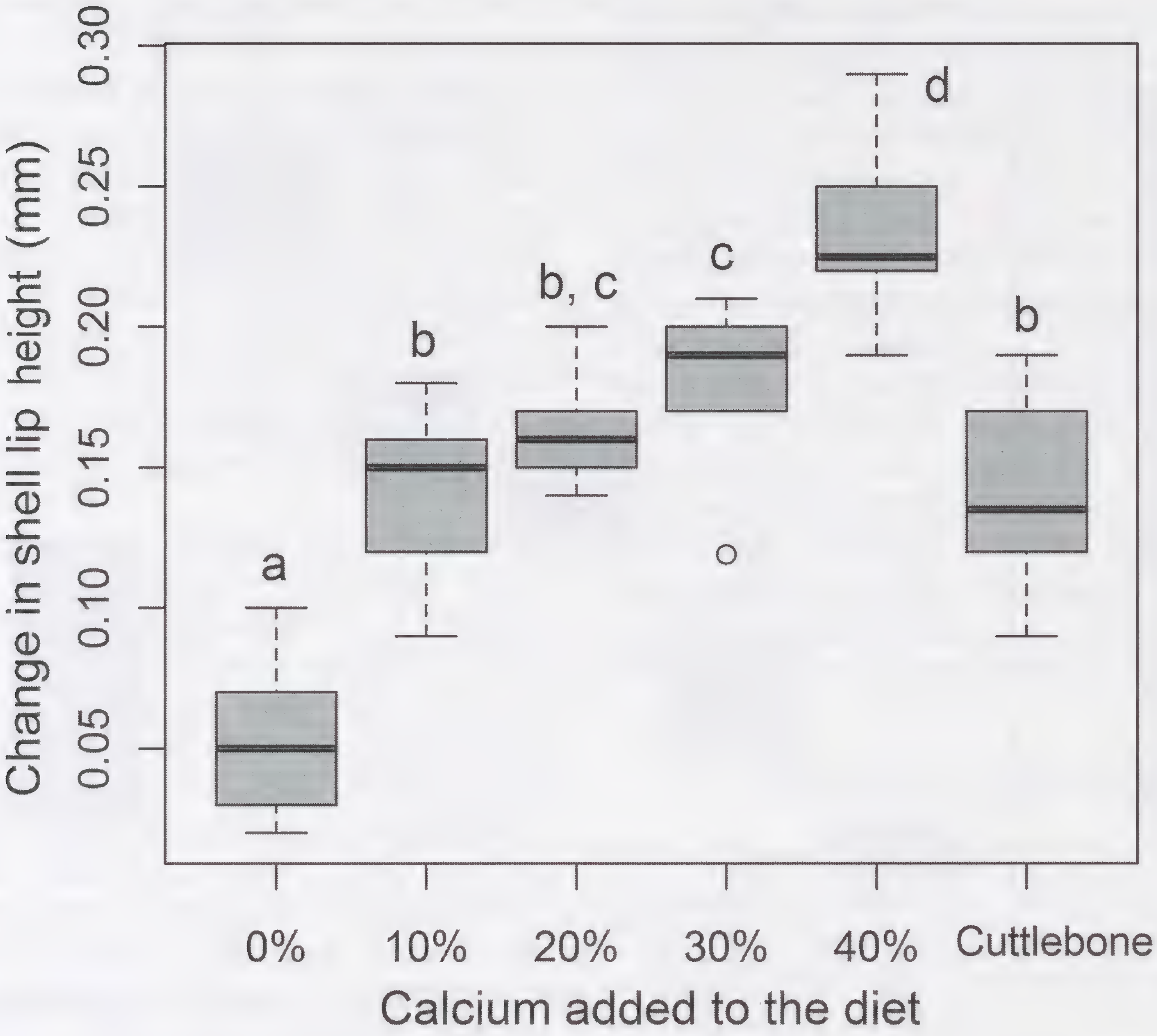

FIG. 6. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the snails' shell lip height.

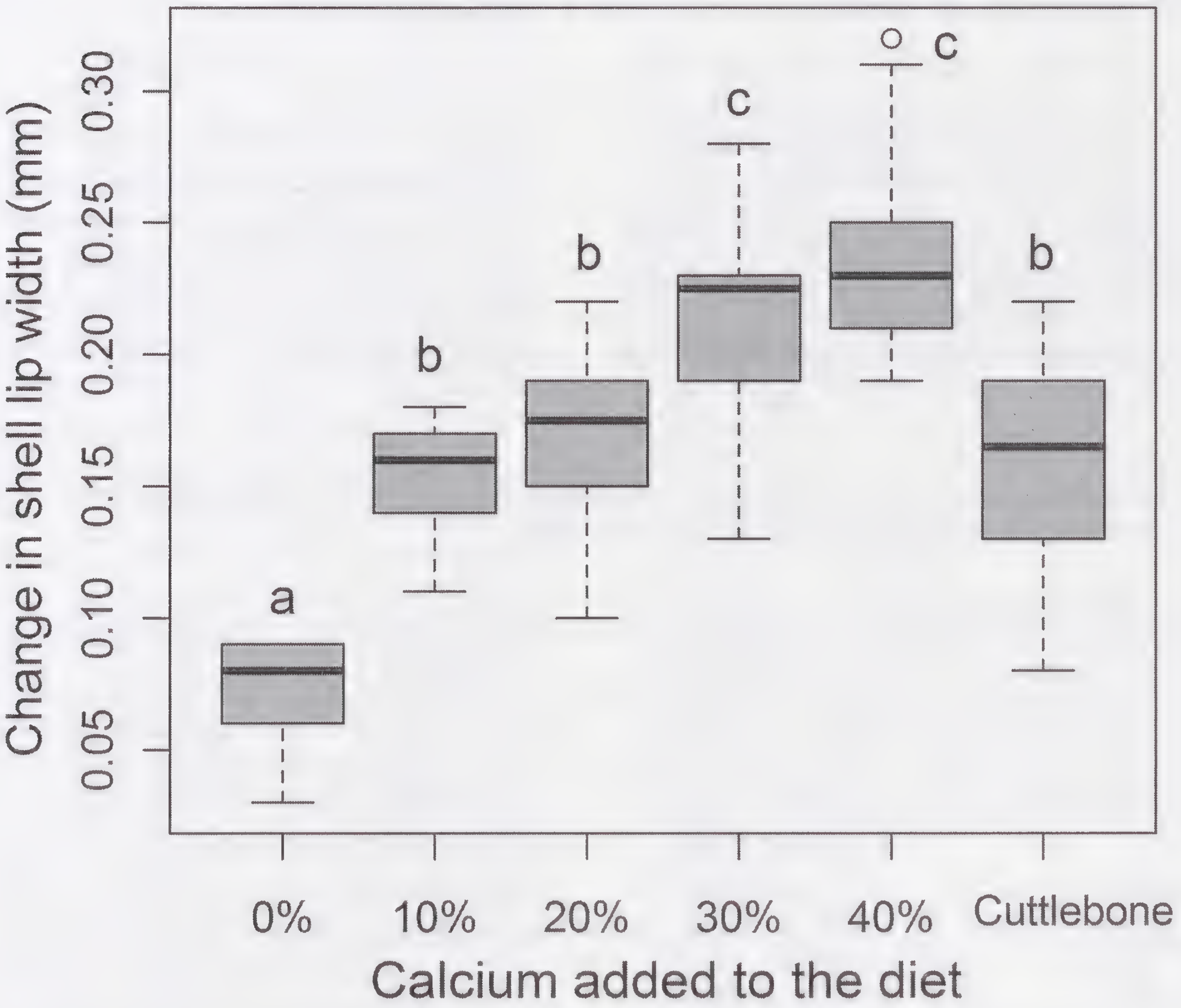

FIG. 7. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the snails' shell lip width.

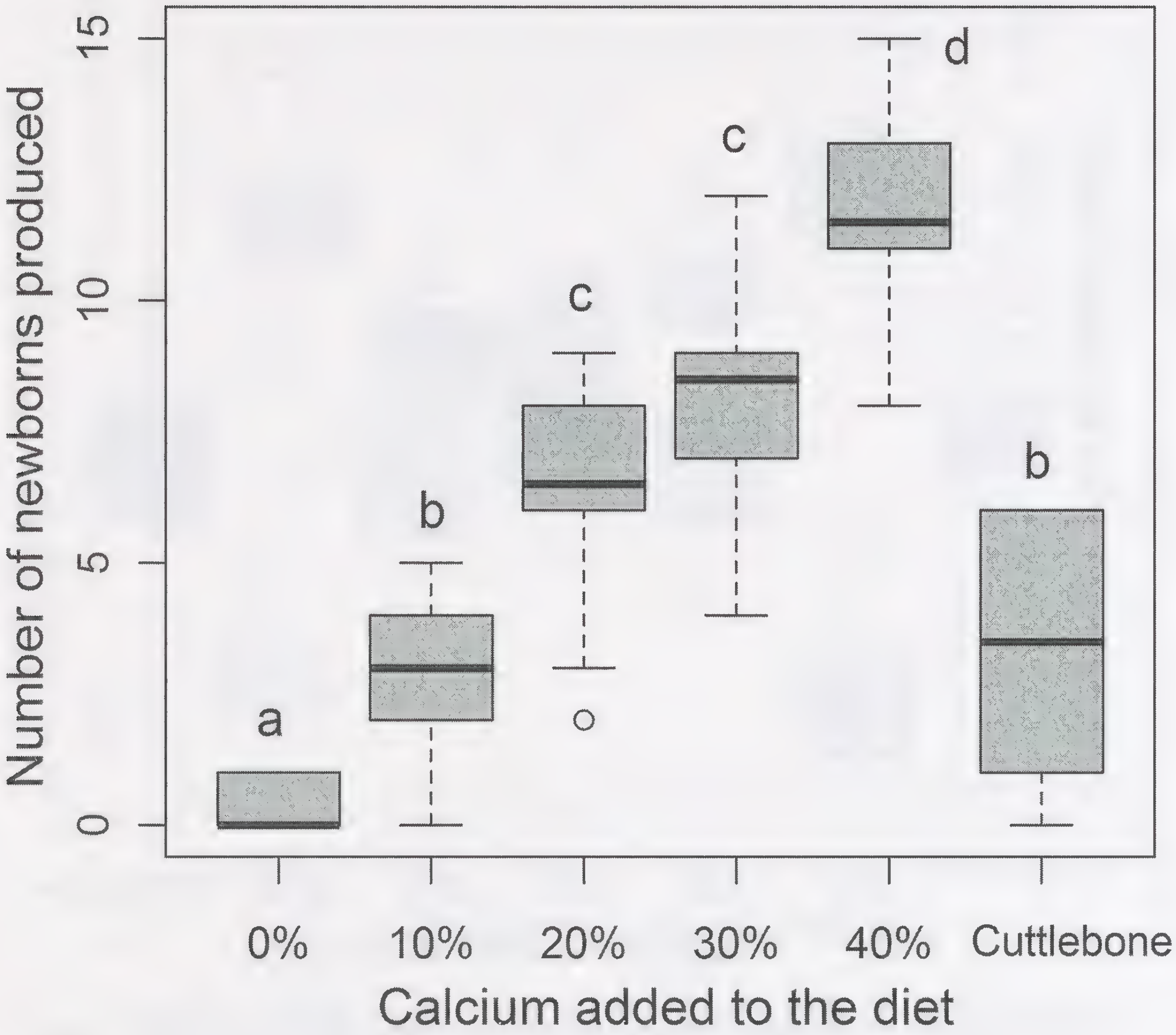

FIG. 8. Effects of different calcium carbonate concentrations added to the diet including powdered cuttlebone on the reproductive success of *Partula gibba,* expressed as number of newborns per month over a year period.

ate to the diet. Nearly all parameters showed an approximately linear relationship.

Visual inspection of the graphs and t-tests showed that the morphometric growth parameters of snails fed 20% added calcium carbonate did not differ significantly from the diet with added cuttlebone (20%) with the exception of their reproductive success where there is a significant difference ($t = 2.9$, $df = 17.986$, $p < 0.01$), the diet with added 20% calcium carbonate has a higher reproduction success than the diet with cuttlebone (20%).

TABLE 1. Linear model summary, for *Partula gibba* morphometric measures and reproduction success against the addition of calcium to the diet.

	F-stats	p-value	r^2	Intercept
Snails' weight	$F_{1,48} = 131.3$	$P < 0.001$	0.73	$P < 0.001$
Shell lip thickness	$F_{1,42} = 215.8$	$P < 0.001$	0.84	$P < 0.001$
Shell height	$F_{1,42} = 75.72$	$P < 0.001$	0.64	$P < 0.001$
Shell width	$F_{1,42} = 108.8$	$P < 0.001$	0.72	$P < 0.001$
Shell lip height	$F_{1,42} = 120.8$	$P < 0.001$	0.74	$P < 0.01$
Shell lip width	$F_{1,42} = 77.45$	$P < 0.001$	0.65	$P < 0.05$
Reproductive success	$F_{1,48} = 223.6$	$P < 0.001$	0.82	ns

DISCUSSION

Nutrition is one of the major factors that affects the performance of livestock (Oluokun et al., 2005). Following this line of thought, this study focused on the importance of calcium in the development and reproduction success of *Partula gibba*. The results presented in this study are consistent with the study performed by Oluokun et al. (2005), which concluded that the snails' shell height, width and thickness increased with an increased calcium concentration in the diet.

Partula snails are nutrient recyclers and hence have an important role in their ecosystem. The total disappearance of *Partula* snails in the wild can be devastating to the ecosystem and further studies on the effect of their extinction upon their ecosystem should be considered. For example, Gärdenfors et al. (1995) noted that the abundance and diversity of snails are closely positively correlated to pH in the soil (Johannessen & Solhøy, 2001). Johannessen & Solhøy (2001) concluded that snail populations have a positive effect upon bird population since some species rely on the snails shell as a source of calcium. These studies indicate the importance of snails as a source of calcium in forest ecosystems.

As *Partula* snails face an uncertain future with the high rate of species extinction currently observed, it is of great importance that all the factors contributing to their welfare are fully understood. This study demonstrated that an increased level of dietary calcium carbonate significantly improved their wellbeing.

Numerous studies previously demonstrated the importance of calcium as a factor determining the development and wellbeing of snails. Fournie & Chetail (1982), for example, established that the addition of calcium carbonate to the snails' diet prevented them from dwarfing, with the exception of snails reared on calcareous soils (Elmslie, 1988; Egonmwan, 2008). Calcium also plays a vital role on the regeneration process of the snails' shell. Bierbauer (1957) reported that shell repair in *Helix pomatia* was enhanced following injection of calcium (Vaidya, 1980). Voelker (1959) noted that scarcity of calcium may result in thinner and more brittle shells, rendering them less fit to protect the snail properly against desiccation, physical damage and invertebrate predators (Johannessen & Solhøy, 2001). Egonmwan (2008) concluded that calcium deficiency in *Limicolaria flammea* resulted in a decrease in the growth rate of these snails raised in the laboratory. All these studies demonstrate that calcium is an important nutrient in the snails' life.

It is therefore recommended that an increase of calcium concentration to 40% instead of 20%, in the standard diet of *Partula* snails would be beneficial and that calcium carbonate powder should be used instead of cuttlebone, since the cuttlebone diet did not demonstrate any additional benefits. It is also known that the cuttlebone can be contaminated with heavy metals (Miramand et al., 2006), such as mercury (Hg) (Lacoue-Labarthe et al., 2009), bioaccumulation of PCBs (Danis et al., 2005) and potentially infectious agents, hence calcium carbonate is effortless to use and it is simpler to control possible routes of contamination that may influence the snails' welfare.

ACKNOWLEDGEMENTS

We are eternally grateful to Dr. Trevor Coote, Dr. Joaquim Hortal, Dr. Tilly Collins, Dr. Arpat Ozgul, Dr. Navinder Singh, Dr. Ana Santos, Jennifer Zanin and Shaheed Macgregor for all the help they provided, also to the "Bugs Team" at London Zoo, and others that helped in anyway.

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Revised ms. accepted 28 February 2011

MALACOLOGIA, 2011, 54(1–2): 147–157

FINE-SCALE INTERTIDAL DISTRIBUTION AND RECRUITMENT PATTERNS OF THE GUMBOOT CHITON *CRYPTOCHITON STELLERI* (POLYPLACOPHORA: MOPALIIDAE)

Joshua P. Lord

Oregon Institute of Marine Biology, P.O. Box 5389, Charleston, Oregon 97420, U.S.A.; lord@uoregon.edu

ABSTRACT

The gumboot chiton *Cryptochiton stelleri* Middendorff, 1847, is the largest intertidal invertebrate herbivore in the northeast Pacific, but little is known about the fine-scale distribution of this species within its range. In this study, extensive intertidal surveys were used to determine the distribution of *C. stelleri* within six rocky intertidal sites on the southern coast of Oregon, USA, and found that gumboot chitons show a patchy and clumped distribution. At all six sites, individuals were found at highest densities within small coves, and small specimens (< 15 cm long) were found almost exclusively in sea urchin pits. Age-frequency histograms were created for populations of *C. stelleri* at all six sites and showed sporadic cohort success, likely as a result of sporadic recruitment. Successful cohorts were indicated by peaks in the age-frequency histograms and were compared between sites in order to determine whether or not successful cohorts occurred at the same time at all sites. There was low similarity between sites, and a negative correlation was found between distance between sites and percent similarity in age-frequency peaks. Combined with other factors, this suggests that larval settlement and cohort success of *C. stelleri* is driven by local factors, not such large-scale factors as upwelling or El Niño.

Key words: population structure, abundance, density, cohort, mollusk.

INTRODUCTION

Intertidal herbivores can have significant ecological impacts on the algal composition and overall species assemblages on rocky shores around the world (Lubchenco, 1978; Moreno & Jaramillo, 1983; Dethier & Duggins, 1984; Jenkins & Hartnoll, 2001). Chitons, such as *Katharina tunicata,* have widespread direct and indirect effects on the population dynamics of the rocky shore by altering macroalgal density (Dethier & Duggins, 1984). *Katharina tunicata* and urchins, such as *Strongylocentrotus purpuratus* and *Strongylocentrotus droebachiensis,* can completely change the surrounding community by causing shifts in habitat type (Leighton et al., 1966; Moreno & Jaramillo, 1983; Himmelman, 1984; Dethier & Duggins, 1984; Chapman & Johnson, 1990). These effects are strongly influenced by population density, since areas of high herbivore density are most dramatically affected (urchin barrens, e.g.).

The ecological impact of high herbivore density highlights the importance of distribution and population structure in community ecology. Density affects not only the food intake of the population, but also its reproductive capacity. Many species must sustain a minimum density in order to be reproductively successful, including barnacles (Kent et al., 2003; Munroe & Noda, 2009), mussels (Downing et al., 1993), urchins (Levitan et al., 1992), and some plants (Kunin, 1997). For example, the sea palm *Postelsia palmaeformis* is unlikely to persist at low population densities due to limited gamete dispersal (Dayton, 1973; Paine, 1988). Density can be especially important for free spawning species, because a critical concentration of sperm is needed for successful fertilization of eggs (Levitan et al., 1992, Young et al., 1992).

Despite the ecological importance of population density and structure for such large intertidal herbivores as *K. tunicata* and *S. purpuratus*, nothing is known about the fine-scale (within site) distribution of the gumboot chiton *Cryptochiton stelleri* Middendorff, 1847 (Petersen & Johansen, 1973; Palmer & Frank, 1974; Yates, 1989). This species is the largest intertidal invertebrate herbivore in the northeast Pacific and is a common inhabitant of rocky intertidal shores from California to Alaska, Kamchatka, and Japan. It is a generalist herbivore, feeding on the blades of algal genera *Mazzaella, Cryptopleura, Nereocystis, Saccharina* and *Ulva*, but preferring *Mazzaella* and *Cryptopleura* (Heath, 1905; Yates, 1989). As such, *C. stelleri* could affect macroalgal abundance in its intertidal and subtidal (down to 60m) habitat and create space for limpets or other grazers in a similar manner to the leather chiton *K. tunicata* (Dethier & Duggins, 1984).

The distribution of *C. stelleri* could be influenced by seasonal changes in food availability, wave action, temperature or other factors (Yates, 1989). Snow (1951) suggested that this species may move to lower intertidal and subtidal areas in the winter and back up in the spring and summer. This type of vertical migration in the intertidal and subtidal zones has been tied to seasonal differences in food availability for the green crab *Carcinus maenas* (Hunter & Naylor, 1993) and several species of limpets (Branch, 1975). Tidal level migration can also occur over a lifetime in some species, such as intertidal snails *Chlorostoma funebralis* (Paine, 1969) and *Monodonta labio* (Takada, 1996). The prevalence of either seasonal or lifetime vertical migration patterns in other mollusks indicates the possibility that these changes in distribution occur with *C. stelleri*.

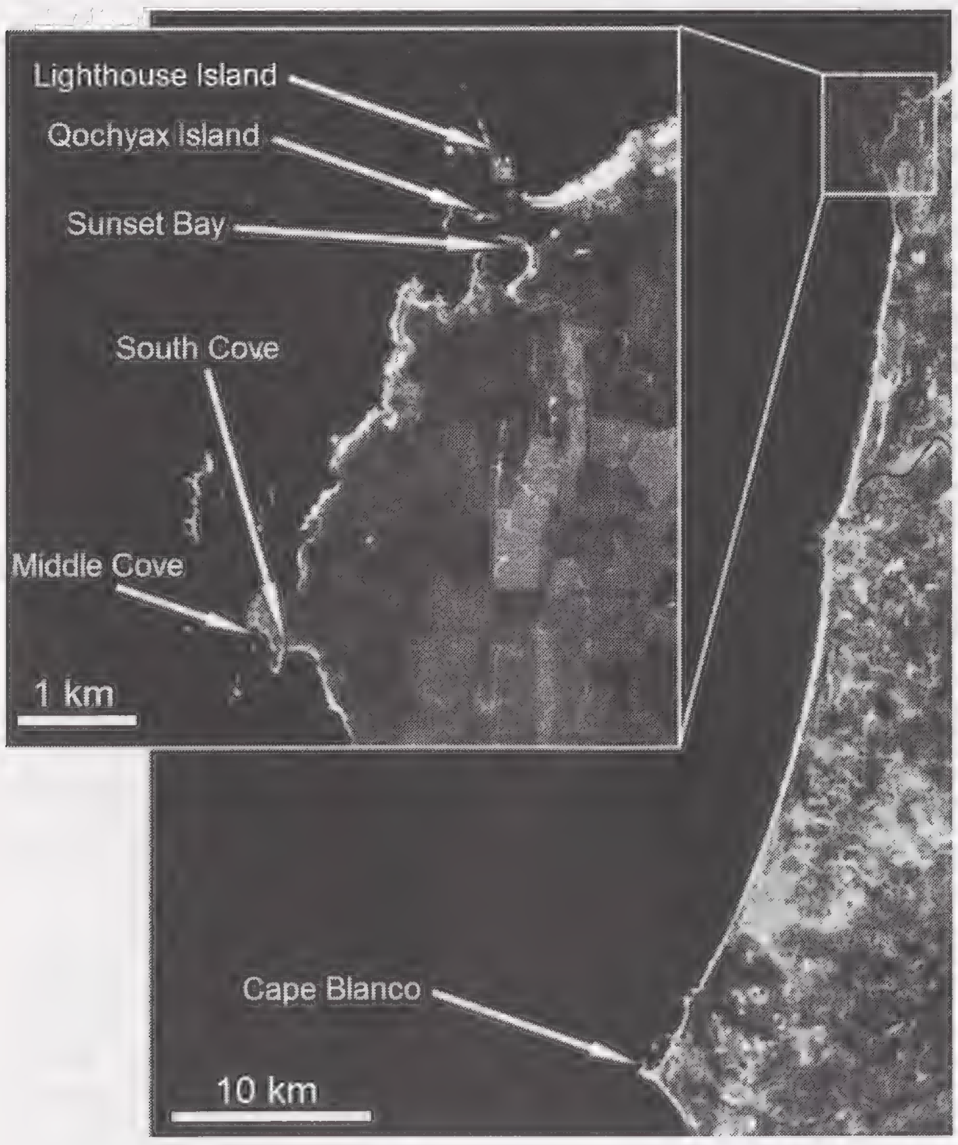


FIG. 1. Locations of all six sites on the southern Oregon coast (north to south): Lighthouse Island, Qochyax Island, Sunset Bay, Middle Cove, South Cove, Cape Blanco.

The present study maps the intertidal distribution of all post-larval life stages of *Cryptochiton stelleri*, including juveniles, which are reportedly extremely rare (Tucker & Giese, 1962; MacGinitie & MacGinitie, 1968; Palmer & Frank, 1974; Yates, 1989). Only 12 individuals less than 15 centimeters in length and only three juveniles were discovered in a five-year feeding study of *C. stelleri* by Yates (1989). The present study also assessed the population structure of several southern Oregon intertidal populations of *C. stelleri*. These distribution and population structure data were used to test the existence of seasonal or ontogenetic vertical migration patterns for this chiton species. The aim of this study was to understand what factors influence the fine scale (within site) intertidal distribution, abundance and recruitment patterns of *Cryptochiton stelleri.*

MATERIALS AND METHODS

Distribution

In order to determine the local distribution, size frequency, and population sizes of *Cryptochiton stelleri* along the southern Oregon coast, surveys were conducted at six sites (Fig. 1). The southernmost of the sites surveyed was Cape Blanco, Oregon (42°50.900'N, 124°33.410'W), a basaltic rocky shore with intertidal areas facing to the northeast, west, and south. All other sites were located just south of Charleston, Oregon (43°18.191'N, 124°23.198'W). Middle Cove of Cape Arago is mostly composed of sandstone boulders and is a relatively protected intertidal area that faces west and has very little foot traffic. South Cove of Cape Arago is a similar intertidal to Middle Cove, though it faces south and has more foot traffic. Sunset Bay is another protected site with high foot traffic and is a small, west-facing bay with a long flat sandstone intertidal bench interspersed with deep tidal channels. Qochyax Island has very little foot traffic and an extensive rocky intertidal area that includes both exposed and protected areas. Lighthouse Island is fairly exposed on the south-facing side and moderately protected on the north-facing intertidal and also has low foot traffic.

The intertidal zones at these sites were sampled from July 2009 to August 2010, on every tide below -0.3 m MLLW, weather-permitting. *Cryptochiton stelleri* were found via extensive (2–3 days per site) systematic searches that were conducted by walking perpendicular to the shoreline from the low water level to the top of the intertidal zone and then back down. With this method, the entire intertidal zone was searched at all sites, since the surveyor passed within 2 meters of every intertidal location. This broad search method was necessary because of the patchy distribution of this species and was appropriate because the goal of this study was to determine distribution over entire sites and not to estimate population size. Once *C. stelleri* were discovered, their exact locations were recorded by triangulation with known landmarks using a compass accurate to 0.1 degrees. This produced coordinates with a maximum error of 1.5 m for the location of each individual. Body volume was then measured to the nearest 5 mL using water displacement in a 4-liter graduated plastic container.

Individual *Cryptochiton stelleri* specimens were tagged at South Cove, Middle Cove, Cape Blanco, and Lighthouse Island in order to detect growth and seasonal movement patterns of individuals. Animals were tagged by inserting zip ties through the edge of the girdle and attaching numbered monel fish tags (National Band and Tag Co.). Zip ties were short (10 cm) and excess tie length cut off after attachment. This method of tagging is similar to that used by Palmer & Frank (1974), who used monofilament line through the girdle and marked with beads. It is also similar to Yates (1989), who used spaghetti tags, also through the girdle. After marking, *C. stelleri* usually rolled up into a ball but resumed normal movement minutes after being placed back in their original location. Individuals were observed until they reattached to the substratum.

Distribution data obtained via triangulation methods were entered using Google Earth® with overlaid infrared aerial photos of the intertidal zone taken by the Oregon Department of Fish and Wildlife (1:7200 scale). These data were then transferred into ArcMap© software and converted into GIS layers. To determine the amount of clumping at different sites, data were analyzed in ArcMap® using the spatial analysis tool "nearest neighbor". This tool calculated the expected mean distances between individuals if their distribution was random and compared this to the observed mean distances between individuals. Getis-Ord General G, another spatial analysis tool, was used to determine if individuals were clustered by size at each intertidal site. This GIS software was also used to analyze variation in distributions at all sites between each sampling date in order to compare tidal and seasonal differences in the distribution of individuals.

To determine whether or not several intertidal predators could consume *C. stelleri*, sea stars *Evasterias troschelii, Pisaster ochraceus,* and *Pycnopodia helianthoides* and crabs *Pugettia producta* and *Cancer productus* were kept together in a 1m x 2m flowing seawater tank for two months with just *C. stelleri* individuals ranging from 10 to 30 cm in length as potential prey items.

Age-Frequency

Volume was converted to age based on data derived from growth lines in the shell plates of *C. stelleri* (Lord, in review). A growth function relating age to volume was fit to these data and was used to estimate age for all surveyed gumboots. Age-frequency histograms were then created for each site and each season and peaks (possible cohorts) in these histograms were compared between sites and sampling dates. Each peak (cohort) in these data were identified using Peakfit® software and major peaks were defined as those at least two times the average number of individuals of each age for each site. Major peaks were then compared between sites in order to determine how uniform recruitment and survival were in *C. stelleri*.

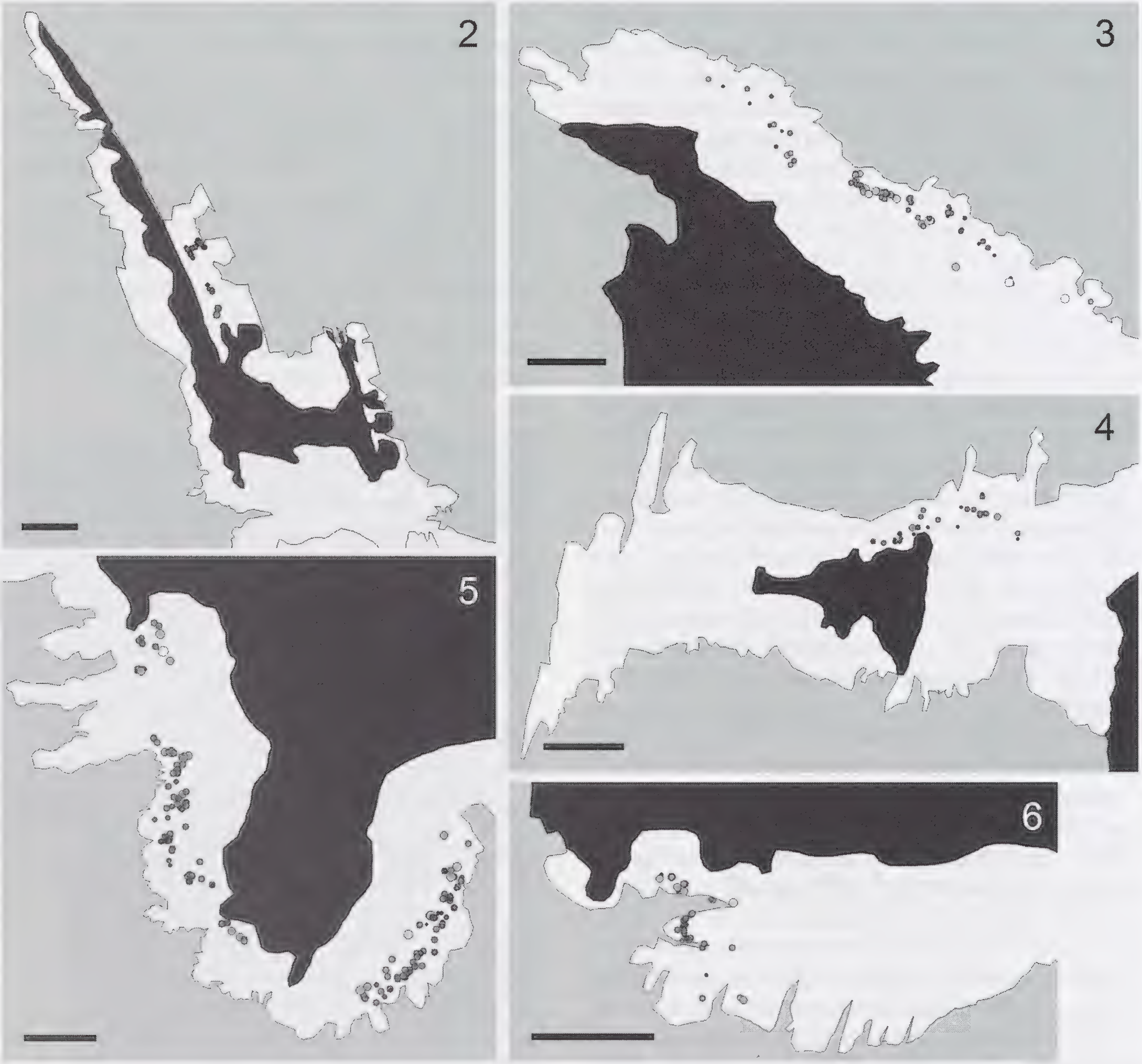
RESULTS

Distribution

Field surveys showed a patchy distribution of *C. stelleri* at all six surveyed sites (Figs. 2–6). Average nearest neighbor distance showed significant ($p < 0.05$) clumping at Cape Blanco, South Cove, Middle Cove, Sunset Bay, and Lighthouse Island. Slightly less clumping was found at Qochyax Island (Fig. 5), but this was likely a result of the small area in which *C. stelleri* was found. Nearest neighbor statistics only included areas where *C. stelleri* was present, so did not take into account large areas where no individuals were found. Qochyax Island had a limited area in which *C. stelleri* was present, but within this area there was not a significant amount of clumping ($p = 0.1$). There were no individuals of this species present in areas of very high wave action at any sites, as none were found in the outer areas of Lighthouse Island (Fig. 2), Cape Blanco (Fig. 3), Cape Arago (Fig. 4), Qochyax Island (Fig. 5) or Sunset Bay (Fig. 6). Gumboot chitons were found almost exclusively in small coves within sites (Figs. 4, 6) or in northeast-facing habitats (Figs. 2, 3, 5).

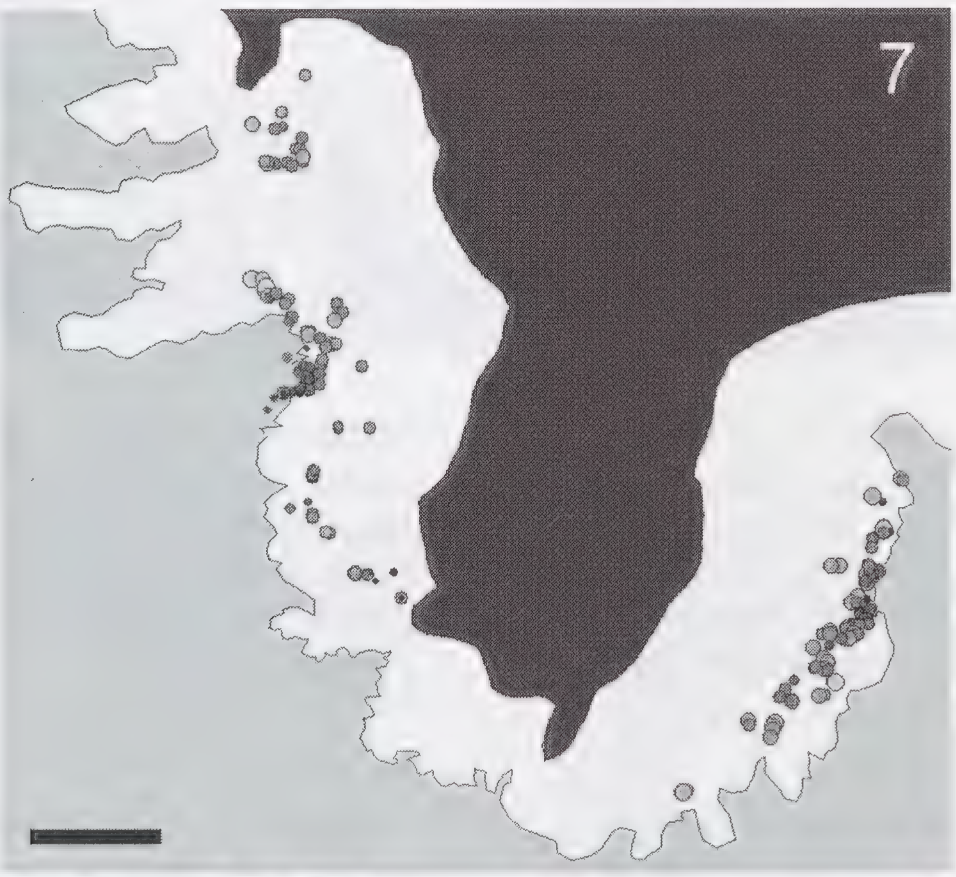
Populations were also clumped based on size at several of the sites (Figs. 2–6). Getis-Ord G High/Low clustering analysis showed significant ($p < 0.05$) clustering of large individuals (by volume) at Qochyax Island, Lighthouse Island, South Cove and Cape Blanco. Clustering based on size was not significant at Middle Cove and Sunset Bay. Few individuals of *C. stelleri* were found in areas of high sand scour, evidenced by the lack of individuals near beaches in the interior of Lighthouse Island, South Cove, Sunset Bay and Cape Blanco.

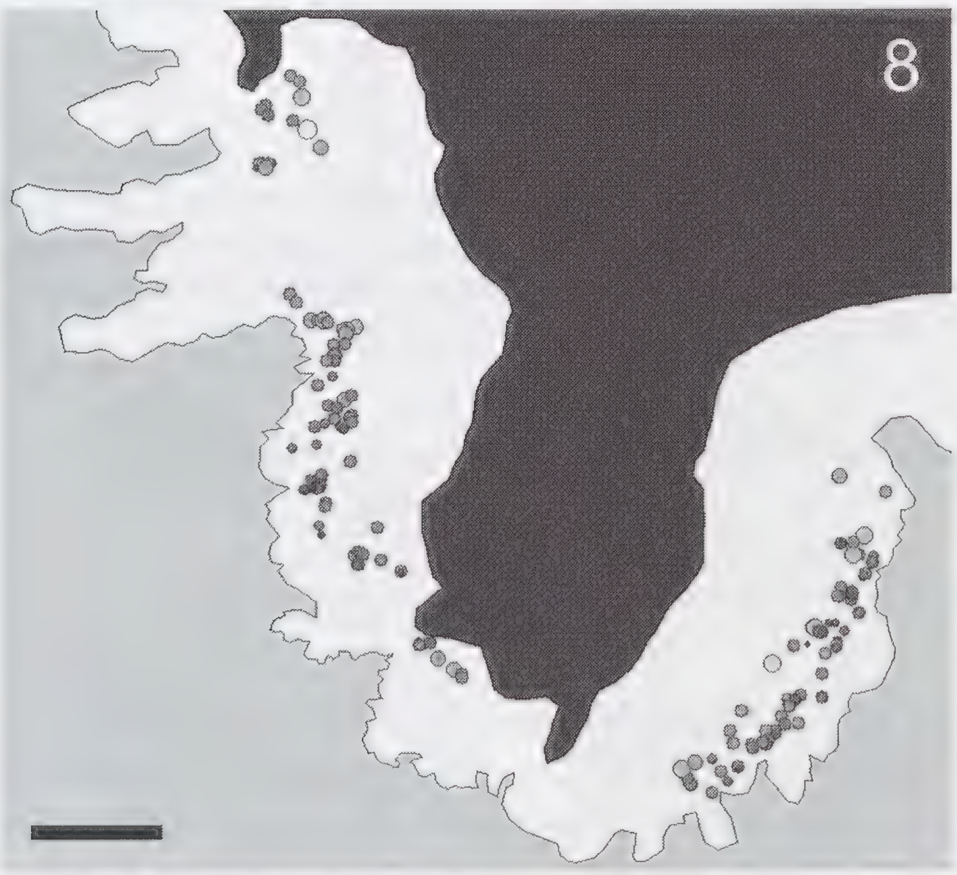
Eighty-five of 92 specimens shorter than 15 cm in length were found in (mostly) abandoned pits of urchins (*Strongylocentrotus purpuratus*) at all six sites. The seven not found in pits were juveniles less than 2 cm in length. Three of



FIGS. 2–6. Size and distribution of *Cryptochiton stelleri* at all sites surveyed in May 2010. Size and lightness of circles are relative to the size of the specimens; small dark circles represent small gumboot chitons and large white circles represent the largest gumboot chitons. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. Scale bar = 50 m. FIG. 2: Lighthouse Island; FIG. 3: Cape Blanco; FIG. 4: Middle Cove (on left) and South Cove (on right) of Cape Arago; FIG. 5: Qochyax Island; FIG. 6: Sunset Bay.

these were in small holes made by boring clams and near the leafy red alga *Cryptopleura*. The remaining four juveniles were on flat surfaces within a bed of *Cryptopleura*, which is their preferred food source (Lord, in press). All juveniles were found below -0.3 m MLLW. Of the over 300 *Cryptochiton stelleri* specimens that were tagged, only 41 were found six months later due to the propensity of the tags to fall out of the girdle. Many specimens were found with marks where a tag had been previously, though they were soon indiscernible because of the rapid healing process of *C. stelleri*. There was not a significant difference between sites in the distance moved between November 2009 and May 2010 recovery, although the range was higher at South and Middle Cove than Sunset Bay. South Cove (n = 19) and Middle Cove (n = 12) chitons had ranges of approximately 3 to 22 meters traveled, while Sunset Bay (n = 9) chitons were between 3 and 12 meters from their initial location.





FIGS. 7, 8. Distribution of *Cryptochiton stelleri* at Middle and South Cove of Cape Arago. Distribution did not change noticeably with season. Scale bar = 50 m. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. FIG. 7: November 2009; FIG. 8: May 2010.

Distributions did not change noticeably at Middle or South Cove of Cape Arago (Figs. 7, 8) or at Sunset Bay (Figs. 9, 10) between November 2009 and May 2010. These three sites are shown because they were the only three surveyed during November due to high wave activity. The "directional distribution" tool in ArcMap® created standard deviation ellipses for each population during each season and these maps indicated that there was no consistent pattern of population movement with season at these site.

In the predation experiment, no *C. stelleri* were eaten by any of the predators over a two-month period. All *C. stelleri* remained attached to the bottom and sides of the tank, never falling off or lying upside-down like they do occasionally in the intertidal zone at low tide. This is relevant, because in the intertidal *C. stelleri* often uses aerial respiration at low tide, during which they expose their gills and often fall off rocks, thus exposing their muscular foot to potential predators.

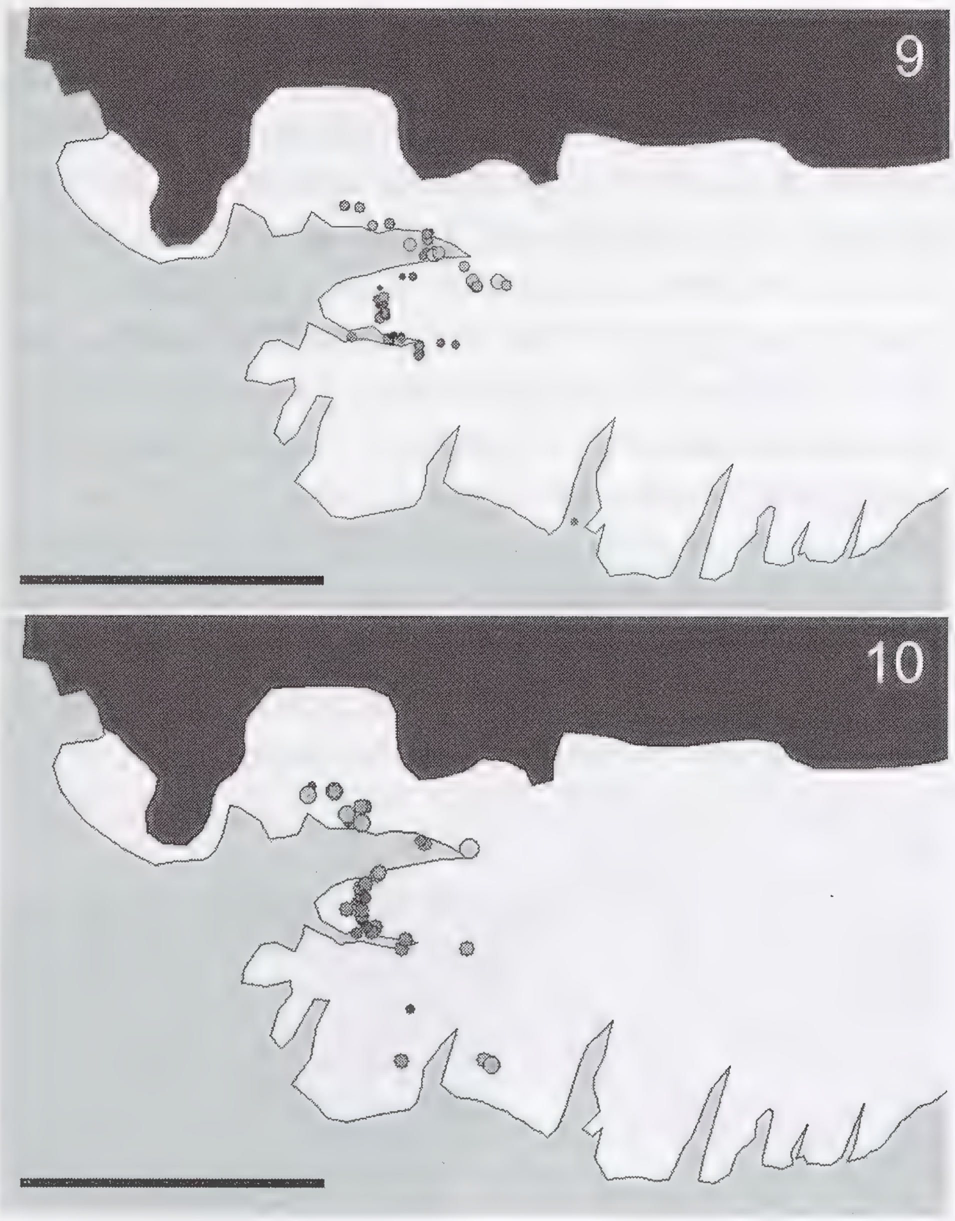
Age-Frequency

All surveyed *Cryptochiton stelleri* specimens were estimated to be between one and 40 years old. These estimates were based on growth curve data (Lord, in review) for *C. stelleri* that show a good regression between age and size. Age-frequency histograms at all sites showed the highest number of individuals at intermediate ages. While close to 100 young (< 15 cm) *C. stelleri* individuals were discovered in all seasons, the cryptic nature of these age classes and their urchin pit habitat makes it very likely that specimens less than 10 years of age are underestimated in these age-frequency histograms. This did not adversely affect peak fitting because relative peaks still appeared at young ages. Major peaks (> 2 x average number) were compared between sites and there was no major peak that was present at a specific age at all sites, although a few peaks were shared by multiple sites (Figs. 11–16). Peaks at 22 and 24 years old were present to some extent at all sites except Cape Blanco. Sunset Bay, Qochyax Island and Lighthouse Island shared a major peak at 16 and 20 years

(Figs. 11, 14, 16). Cape Blanco, Middle Cove, and Sunset Bay shared peaks at 30 years (Figs. 12, 13, 16) but few other peaks were shared between more than two sites. Distance was measured as a straight line between sites, and similarity was calculated as the number of shared peaks over the number of total peaks for each pair of sites.

There was a significant correlation between the number of shared peaks and the $\log_{10}$ of distance between sites (Pearson's correlation coefficient, $r^2 = 0.46$, $t = -3.34$, $df = 13$, $p < 0.01$) (Fig. 17). The distances were $\log_{10}$ transformed because all of the sites were relatively close together with the exception of Cape Blanco, which would make a test of correlation impossible. The two sites with the highest percentage (66%) of peaks in common were Sunset Bay and Qochyax Island, which were the closest sites to each other, at 0.37 km (Table 1). The second most similar sites (60%) were South Cove and Middle Cove of Cape Arago, which were 0.38 km apart. The northern-most site, Lighthouse Island, did not share any peaks with the southern-most site, Cape Blanco. Cape Blanco only shared an average of 21% of its age-frequency peaks with other sites, all of which were at least 50 km north of Cape Blanco. The closest site to the north of Cape Blanco was South Cove, which was the most similar site to Cape Blanco in terms of age-frequency peaks, at 40% (Fig. 17, Table 1).

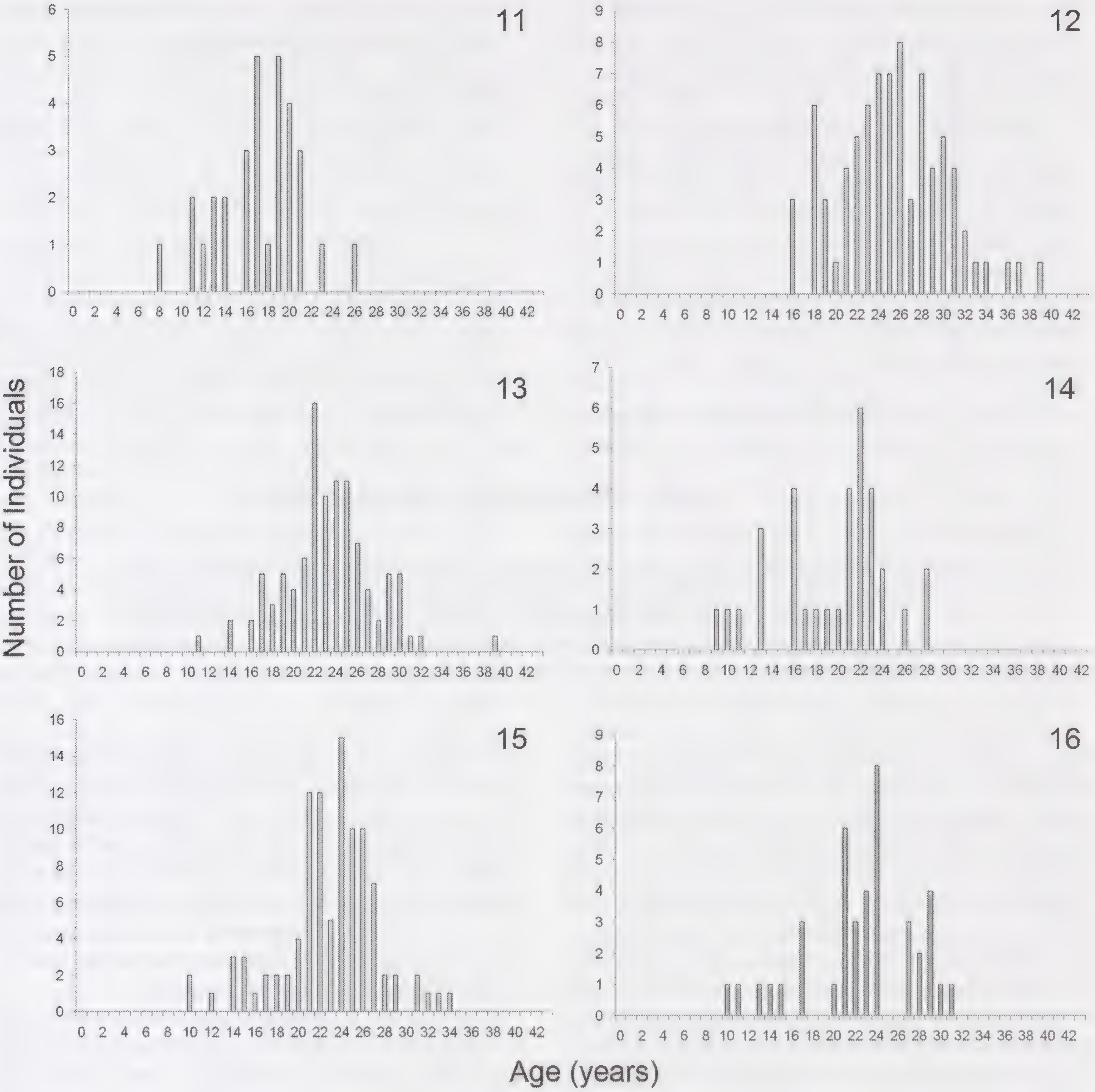
No correlation ($p > 0.4$) was found between upwelling start date or strength and age-frequency histogram peaks or gaps. There was also no correlation ($p > 0.4$) between El Nino years and the peaks or gaps in age-frequency histograms at any of the sites.



FIGS. 9, 10. Distribution of *Cryptochiton stelleri* at Sunset Bay. Like at Cape Arago, distribution did not change noticeably between seasons. Scale bar = 50 m. Light gray fill represents the ocean, white is intertidal, and dark gray is terrestrial. FIG. 9: November 2009; FIG. 10: May 2010.

TABLE 1. Distances and similarities in age-frequency peaks between six different sites on the southern Oregon coast. There is a significant negative correlation between the distance and similarity between sites. Sites are arranged north to south in both columns and rows, with Lighthouse Island the northernmost site and Cape Blanco the southernmost.

Sites	Lighthouse Island	Qochyax Island	Sunset Bay	Middle Cove	South Cove	Cape Blanco	
		0.58	0.89	4.67	4.83	57.9	Distance (km)
Lighthouse Island	X	*0.44*	*0.22*	*0.44*	*0.22*	*0.00*	*Similarity (%)*
			0.37	4.19	4.25	57.3	Distance (km)
Qochyax Island		X	*0.66*	*0.22*	*0.22*	*0.22*	*Similarity (%)*
				4.00	4.07	57.06	Distance (km)
Sunset Bay			X	*0.40*	*0.40*	*0.20*	*Similarity (%)*
					0.38	53.2	Distance (km)
Middle Cove				X	*0.60*	*0.20*	*Similarity (%)*
						53.1	Distance (km)
South Cove					X	*0.40*	*Similarity (%)*



FIGS. 11–16. Age-frequency histograms for all six sites surveyed in May 2010. No peaks are shared between all sites, although most sites have a peak at around 20–22 years. The lack of young individuals is partially a result of their cryptic nature. FIG. 11: Lighthouse Island; FIG. 12: Cape Blanco; FIG. 13: Middle Cove; FIG. 14: Qochyax Island; FIG. 15: South Cove; FIG. 16: Sunset Bay.

DISCUSSION

The patchy distribution of *Cryptochiton stelleri* at each of six sites (Figs. 2–6) raises several questions about the life history and ecological impact of this species. It is not surprising that *C. stelleri* specimens were not found in areas of high wave action or high sand scour because these types of habitat generally do not have the types of thin bladed seaweeds upon which *C. stelleri* feeds. In addition, *C. stelleri* does not clamp to the substratum with the same force and tenacity that *Katharina tunicata* or other wave-tolerant chitons do, and is often found unattached to the substratum at low tide (pers. obs.). Therefore, it is likely that both physical and dietary limitations result in the absence of *C. stelleri* in areas of high wave action or sand scour.

However, the clumped distribution of *C. stelleri* found by this study was present at sites where this species is abundant (Figs. 2–6), so the clumped distribution is not likely due to sand scour or extreme wave action. Sand

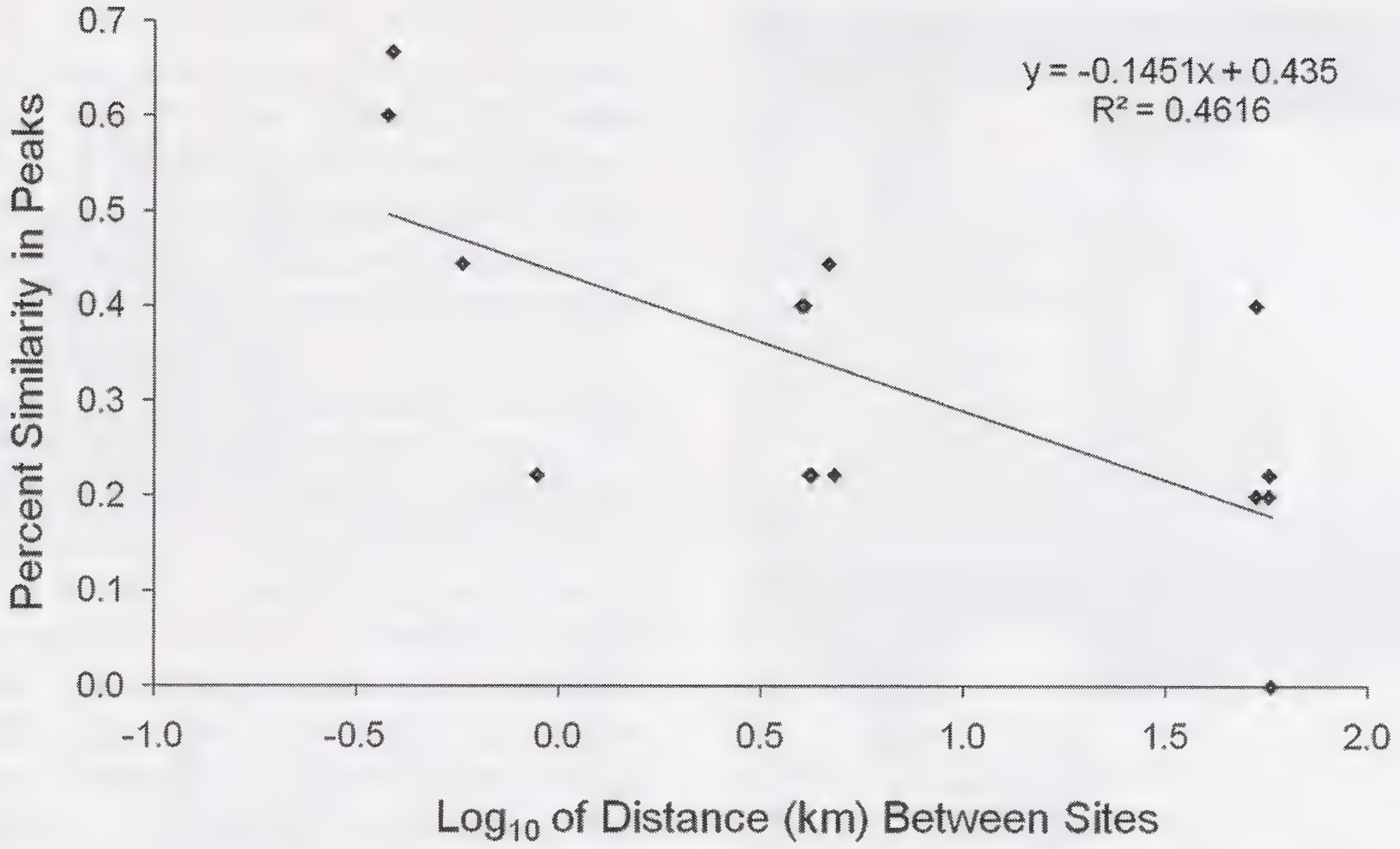


FIG. 17. Distances ($\log_{10}$ km) and similarity in age-frequency peaks between six different sites (15 pairs of sites). Distances were $\log_{10}$ transformed in order to compare between sites since five sites were relatively clumped (within 10 km) and the sixth site was approximately 55 km south of the others. Correlation coefficient and equation of the best fit line are shown.

scour generally occurred at the edges of the surveyed sites and wave action is similar within protected sites, so these factors are not likely to influence distribution within these sites. A clumped distribution is not unusual for chitons (Grayson & Chapman, 2004; Connelly & Turner, 2009). During spring, summer and fall, leafy red algae such as *Cryptopleura* and *Mazzaella splendens* and greens such as *Ulva lactuca* are abundant throughout all sites surveyed. Therefore, the clumped distribution of *C. stelleri* is not due to food distribution. Distribution patterns are also unlikely to be driven directly by predation, since *C. stelleri* was not eaten by any predator. Sea stars *Evasterias troschelii, Pisaster ochraceus,* and *Pycnopodia helianthoides* and crabs *Pugettia producta* and *Cancer productus* did not feed on *C. stelleri* in this study, though field observations have been made of sea stars consuming *C. stelleri*. It is likely that sea stars and crabs can consume *C. stelleri* if it becomes detached from the rocks, exposing the muscular foot.

It seems more likely that *C. stelleri* is limited to protected areas even within sites in order to avoid being dislodged from the rocks. Dislodgement could result in mortality from wave action or increased predation risk. Gumboot chitons were most common in small coves within sites, especially at Lighthouse Island (Fig. 2), Middle Cove (Fig. 6), and Sunset Bay (Fig. 4). Because *C. stelleri* under 15 cm in length were found almost exclusively in abandoned sea urchin pits, it is also possible that the distribution of small *C. stelleri* is driven by the presence of these pits. With smaller individuals limited to these cryptic habitats and large individuals able to move at least 20 meters, this could explain the clumping of large individuals in areas where small specimens are not present.

The cue for settlement and metamorphosis for *C. stelleri* is encrusting coralline algae (Lord, in press), which is ubiquitous throughout all sites so is not a limiting factor in the settlement or recruitment of *C. stelleri*. However, urchin pits are largely covered in encrusting coralline algae because of macroalgal grazing by *S. purpuratus* and could serve as a good spot for *C. stelleri* to settle and survive. The small coves with high densities of *C. stelleri* could be acting as larval traps where slower, swirling water allows larvae to settle out of the water column. Settlement and recruitment in small coves may also lower mortality rates of new recruits and juveniles which are undoubtedly susceptible to wave bashing. If urchin pits act as a nursery for young individuals, this would explain the pattern of large *C. stelleri* being clumped, since areas without urchin pits are only going to be occupied by large individuals that have moved there later in life. Clumps of large individuals could have a great impact on macroalgal abundance at least on a fine scale, given that smaller herbivores, such as *Katharina tunicata* (Dethier & Duggins, 1984) and *Strongylocentrotus purpuratus* (Leighton, 1966; Estes & Duggins, 1995) can greatly affect algal assemblages. Seaweed consumption could be especially high in these adult high density areas because *C. stelleri* food intake scales linearly with body volume (Lord, in review).

While *C. stelleri* will move out of the urchin pits over the course of their lives, they do not display seasonal variation in distribution (Figs. 7–10) and do not move up or down in the intertidal with age. Snow (1951) mentioned that *C. stelleri* move down in the intertidal during the winter and then up during the spring. This has been described in a variety of other species, including crabs (Hunter & Naylor, 1993) and several species of limpets (Branch, 1975). However, year-round surveys in the present study did not reflect this pattern at any of these southern Oregon sites. There were also no vertical patterns in size or age of *C. stelleri* like those shown in *Chlorostoma funebralis* (Paine, 1969) and *Monodonta labio* (Takada, 1996). The lack of vertical migration with season by *C. stelleri* may be due to its ability to go months without eating (Yates, 1989) or to the fact that it already inhabits fairly protected habitats. By living in protected areas, there may be no need for *C. stelleri* to move up or down in the intertidal zone to avoid the intense wave action from winter storms in Oregon.

More about larval settlement patterns can be ascertained from age-frequency data (Figs. 11–16) for each site and similarity in cohort peaks within age-frequency distributions between sites (Table 1). The success of these large cohorts (peaks) could be due to high recruitment or to low mortality at some life stage. It is unlikely that predation on adults would vary greatly between cohorts, so the most likely causes of the variation between cohort sizes are differences in settlement or juvenile survival. While predation experiments have not been done with juvenile *C. stelleri*, it is likely that crabs and sea stars or even fish could easily detach and consume these small individuals with tiny plates. Therefore, a good recruitment year for any of these predators could cause high juvenile mortality for *C. stelleri*. However, population levels of *C. stelleri* are not very high compared to other species of mollusks and young individuals are found in small protective pits, so it is unlikely that any life stage of *C. stelleri* is the primary food source for any predator.

Therefore, the most likely cause of variations in cohort size is larval supply and settlement success. This species of chiton spawns annually (Tucker & Giese, 1962; Lord, in press) and has lecithotrophic larvae. Differences in number of planktonic predators could have an impact, since larvae can remain competent for up to two months even though they can settle and metamorphose in as few as five days after spawning (Lord, in press). Oceanographic conditions, such as the directions of currents, could affect settlement as well, as could wave action or other small-scale near-shore oceanography conditions. For example, populations may have successful self-recruitment when local barriers form and limit the movement of planktonic larvae out of a cove or bay. At several sites along the southern Oregon coast, upwelling can cause these barriers to form at the mouths of such coves as Sunset Bay, potentially trapping larvae inside and enhancing local recruitment (Shanks & McCulloch, 2003).

Shared peaks in cohort size between sites could be a result of either large-scale dispersal of larvae to multiple sites in the same period or local oceanographic conditions that enable successful settlement at multiple sites. No peaks were shared between all sites, and very few peaks were shared by more than three of the six sites, suggesting that successful cohorts were not driven by large-scale oceanography, because if that were the case then all sites would likely share peaks in the age-frequency histograms. There was also no correlation between upwelling strength or start date and the age-frequency histogram peaks or gaps. This suggests that local conditions are more likely to affect the success of a recruitment class or cohort. The significant negative correlation between the number of shared cohort peaks and distance between sites further supports this conclusion (Fig. 17). The high similarity in peaks between the closest sites (Middle Cove + South Cove, Sunset Bay + Qochyax Island) indicates that these sites either share larvae or have similar near-shore local oceanographic patterns (Table 1). There appears to be low population connectivity between sites, given the potentially short larval period of this species and the lack of shared peaks in age-frequency histograms, although genetic work is necessary to confirm this.

Limited larval supply, settlement, or high post-settlement mortality could also partially explain the relative scarcity of small *C. stelleri* reported by multiple studies (Tucker & Giese, 1962; MacGinitie & MacGinitie, 1968; Palmer

& Frank, 1974; Yates, 1989). However, these studies report a lack of individuals < 15 cm in length, or < 13 years old (Lord, in review), a span of ages too wide to be accounted for by sporadic recruitment. The present study found over 90 individuals in this "rare" size range, with several at every site, and almost all of them were in sea urchin pits or other holes in the rocks. In areas without sea urchin pits, young *C. stelleri* presumably occupy crevices or live under rocks in the low intertidal zone. It is very likely that the use of these cryptic habitats by young individuals is the reason why they are not found often. Juvenile *C. stelleri* are yellow unlike the dark red adults, which may also cause confusion.

Surveys in this study showed that the different life stages of *C. stelleri* prefer different microhabitats, with young (< 13 years) individuals occurring in cryptic habitats. They may choose these habitats to avoid predation or to avoid wave action, but their preference for these habitats coupled with the relatively low mobility of adults may enhance the clumped distribution of this species. Spatial and temporal differences in abundance and distribution are most likely a result of differential settlement and juvenile survival that are controlled by nearshore oceanography or other local factors. The resulting patchy distribution of *C. stelleri* may result in locally high algal consumption in areas of high density of this species within sites.

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Revised ms. accepted 13 January 2011

MALACOLOGIA, 2011, 54(1–2): 159–202

NATURAL HISTORY OF TURRITELLINE GASTROPODS (CERITHIODEA: TURRITELLIDAE): A STATUS REPORT

Warren D. Allmon

Paleontological Research Institution and Department of Earth & Atmospheric Sciences,
Cornell University, 1259 Trumansburg Road, Ithaca, NY 14850, U.S.A.;
wda1@cornell.edu

ABSTRACT

A new review of available information, published and unpublished, on the biology and paleobiology of turritelline gastropods expands our knowledge of this important group, which is among the most abundant and widespread marine gastropod clades of the past 130 million years. It also highlights many areas in which additional research is needed.

Living turritellines are mainly sessile, semi-infaunal suspension feeders, in shallow waters of full-marine salinity and temperatures below 20°C, but they can occasionally be more active and diverse in their habits, crawling on the surface and thriving in a variety of depths, salinities, and temperatures. They are eaten by a surprising diversity of predators, and infected by numerous parasites, especially trematodes, but little is known about interactions with predators, parasites, competitors, or commensals in nature. Their reproductive patterns (broadcast spawning and spermatophores) appear to depend on high abundance, which may help explain why they are the dominant species in many marine communities. The larvae of most species float (or swim) and feed in the plankton for no more than 2 weeks, but nothing is known about settlement. Several fossils and at least one modern species are brooders. Spermatozoa are dimorphic, and frequently paired and/or multiflagellate.

Soft anatomy is known for only a few species, and ranges of variation remain largely undocumented. Radulae in particular have been strangely neglected, and this paper presents only the second published SEM image of a turritelline radula. Shell growth rates are variable but can be relatively rapid. Most species appear to live less than three years. Little is known about shell function or development. Although there is strong evidence for a positive correlation of abundance with available nutrients and/or primary productivity, this has not been examined quantitatively or experimentally.

Gathering such natural history information on marine gastropod groups should be as high a priority as systematic and phylogenetic analyses. Information scattered in the literature is now much more available via internet search tools, and this approach should be used for other groups.

Key words: predation, spermatozoa, reproduction, radulae, feeding, parasites.

> "*Perhaps the strongest argument in support of natural history is simply the magnitude of our current ignorance about nature. ...*"
>
> (Wilcove & Eisner, 2000)

INTRODUCTION

The current crisis in systematics has been frequently noted (Winston, 1992; Feldmann & Manning, 1992; Savage, 1995; Wilson, 2004; Agnarsson & Kuntner, 2007; Wheeler, 2010): there are not enough systematists to describe and interpret the diversity of life that is rapidly disappearing. Less widely appreciated is the equally dire need for documentation of natural history – the basic biology of species. Although it is frequently seen as old-fashioned and far from cutting-edge science by both the public and many scientists, natural history is still the crucial basis for almost all organismal (and much sub-organismal) biology, from systematics and behavior to ecology and genetics. Many fundamental biological questions and pressing societal problems – from evolution to natural product prospecting to conservation – cannot be addressed without more and better basic natural history information (Bartholomew, 1986; Greene, 1986, 2005; Futuyma, 1998; Grant, 2000; Wilcove & Eisner, 2000; Dayton, 2003).

In this context, turritelline gastropods (Family Turritellidae, subfamily Turritellinae, mostly *sensu* Marwick, 1957a, b; Table 1) are certainly among those groups that deserve detailed documentation of their natural history. Turritelline shells are not large and showy (as are, e.g., members of Volutidae or Faciolariidae), nor are they of great economic importance (e.g., Strombidae or Haliotidae); they are neither among the most diverse marine gastropod groups (e.g., Turridae or Conidae), nor the subject of intense ecological study (e.g., Littorinidae). Yet turritellines are among the most important gastropod groups of the past 130 million years. Paleontologically, they are one of the most abundant, geographically widespread,

TABLE 1. Generic and subgeneric names that have been used for living and fossil species in the family Turritellidae. Subfamily classification modified slightly from Marwick (1957a, b).

Taxon	Authority	Age
Subfamily Turritellinae		
Acutospira	Kotaka, 1959	Eocene
Amplicolpus	Marwick, 1971b	Paleocene-Miocene
Archimediella	Sacco, 1895	Oligocene
Bactrospira	Cossmann, 1912	Pliocene
Callostracum	Smith, 1909	Recent
Calvertella	Petuch, 1988	Miocene
Coeloconica	Eames, 1957	Eocene
Colposigma	Finlay & Marwick, 1937	Paleocene
Colpospira	Donald, 1900	Eocene-Recent
Colpospirella	Powell, 1951	Recent
Costacolpus	Marwick, 1966	Late Cretaceous
Cristispira	Allison, 1965	Eocene
Ctenocolpus	Iredale, 1924	Miocene-Recent
Eurytorus	Gardner, 1947	Miocene
Gazameda	Iredale, 1924	Miocene-Recent
Hataiella	Kotaka, 1959	Oligocene-Miocene
Haustator	Montfort, 1810	Eocene-Recent
Idaella	Kotaka, 1959	Miocene
Kapalmerella	Allmon, 2005	Paleocene-Eocene
Kurosioia	Kotaka, 1959	Pleistocene
Leptocolpus	Finlay & Marwick, 1937	Paleocene
Maoricolpus	Finlay, 1926	Oligocene-Recent
Mariacolpus	Petuch, 1988	Miocene
Neohaustator	Ida, 1952	Pliocene-Recent
Nipponocolpus	Kotaka, 1959	Recent
Peyrotia	Cossmann, 1912	Miocene
Platycolpus	Donald, 1900	Recent
Reymentella	Adegoke, 1977	Paleocene
Sechuritella	Olsson, 1944	Late Cretaceous
Spirocolpus	Finlay, 1926	Eocene

(continues)

(continued)

Taxon	Authority	Age
Springvaleia	Rutsch, 1942	Miocene
Stiracolpus	Finlay, 1926	Pliocene-Recent
Torcula	Gray, 1847	Eocene-Recent
Torculoidella	Sacco, 1895	Pliocene
Torquesia	Douvillé, 1929	Cretaceous-Eocene
Tropicolpus	Marwick, 1931	Oligocene
Turritella	Lamarck, 1799	Cretaceous-Recent
Vermicularia	Lamarck, 1799	Pliocene-Recent
Wyatella	Adegoke, 1977	Eocene
Zeacolpus	Finlay, 1926	Pliocene-Recent
Subfamily Protominae		
Protoma	Baird, 1870	Miocene-Recent
Protomella	Thiele, 1931	Recent
Subfamily Pareorinae		
Craginia	Stephenson, 1952	Late Cretaceous
Mesalia	Gray, 1847	Paleocene-Recent
Motyris	Eames, 1952	Eocene
Pareora	Marwick, 1931	Oligocene
Sigmesalia	Finlay & Marwick, 1937	Eocene
Tachyrinchella	Titova, 1994	Oligocene
Tachyrhynchus	Mörch, 1868	Recent
Woodsalia	Olsson, 1929	Eocene
Zaria	Gray, 1847	Recent
Subfamily Turritellopsinae		
Glyptozaria	Iredale, 1924	Recent
Kimberia	Cotton & Woods, 1935	Recent
Orectospira	Dall, 1925	Recent
Turritellopsis	Sars, 1878	Recent

and recognizable marine macrofossil groups of the Cretaceous and Cenozoic: they occur as fossils on every continent and in almost all marine deposits since the Early Cretaceous, and are frequently the dominant or even the sole macrofossil in assemblages in which they occur (reviewed in Allmon, 1988, 2007). This rich fossil record reveals that at least some turritelline species evolve rapidly compared with many other gastropods (Kauffman, 1972, 1977). For all of these reasons, turritellines are among the most biostratigraphically useful molluscan groups for this time interval (Woodring, 1930, 1931; Gardner, 1935; Stenzel, 1940; Kauffman, 1977; Sohl, 1977; Saul, 1983; Squires, 1988). Because of their widespread occurrence, fossil turritellines have been used frequently for paleoenvironmental analysis via stable isotopes (Andreasson & Schmitz, 1996, 1998, 2000; Jones & Allmon, 1999; Schmitz & Andreasson, 2001). Living turritelline species occur widely throughout much of the world's seas, and are among the most abundant gastropods in many places where they occur (reviewed in Allmon, 1988). Recent compilations (Vos & Gofas, 2009; Allmon, 2010) record approximately 1,700 fossil and living species and subspecies names, which may translate into as many as 150 valid living and perhaps 800 valid fossil species. Turritellines are also of evolutionary interest because they are one of a small number of gastropod clades that has apparently independently developed suspension feeding (DeClerck, 1995). Humans and turritellines are also interconnected in a number of ways. Turritellines are locally important for artisanal fisheries, especially in parts of Asia, and are exploited for the shell trade in many areas (both of these uses are underdocumented; Carpenter & Niem, 1998: 455–457). Several living species have been used as bioindicators for trace metal accumulation (Langston et al., 1999; Paul et al., 1999; Gibbs et al., 1998). At least one turritelline species (*Maoricolpus roseus* in Australia) is a serious invasive (human-introduced) pest (Bax et al., 2003; Gunasekera et al., 2005), and several others may be in serious decline as a result of human activities (Allmon, in review).

Our understanding of the basic biology of the Turritellinae, however, has not kept pace with recognition of its ecological, evolutionary, and geological importance. Ironically, this was probably in part because something *was* known about it. Until relatively recently, the ecology and environmental occurrence of modern turritellines was believed to be well understood and not very variable (Graham, 1938; Yonge, 1946). Closer examination, however, shows turritellines to be much more diverse. Although living turritellines are mostly suspension feeders and most abundant within a relatively narrow range of environmental conditions, the behavior, ecology, and environmental occurrence of the group are more heterogeneous than previously thought (Allmon, 1988), and the group has probably changed its environmental tolerances during its history (Allmon, 1992, 2007).

Living turritellines are not particularly easy animals to study. Adults are sensitive to exposure to air (Avens & Sleigh, 1965) and high temperatures (pers. obs.), which makes them difficult to transport from the field to aquaria. They are also extremely difficult to raise from eggs beyond the late veliger stage (Wright, 1956; Probst & Crawford, 2008). Despite these difficulties, however, a great deal of information exists about numerous aspects of their biology and paleobiology, although most of it is widely dispersed in the literature. More than two decades ago, I summarized the then-current state of knowledge of the ecology of living species of the group, based on both the scattered published sources and new observations (Allmon, 1988). Since then, considerable new information has become available on the biology of many living and fossil turritellines. Of equal or greater importance, the maturation of internet databases and search tools has made compilation of natural history information much easier than ever before. I have therefore been able to locate isolated bits of data, such as stomach contents of predators, in sources that would otherwise likely have never come to my attention. Utilizing these search tools in this way is a major, but so far underexploited, research approach for biologists.

The present paper is thus not only an update and expansion of that earlier review, it is also an attempt to stimulate other workers to produce similar reviews of the natural history of other marine gastropod groups. Only a few such surveys exist (Thompson, 1958; Paine, 1965; Ghiselin & Wilson, 1966; Peron & Turner, 1977; Harasewych, 2002; Trowbridge, 2002). As a consequence, malacologists and other biologists lack easy access to information that could be of enormous value in developing and testing ideas about the ecology, conservation, evolution, and other areas of biology of one of the most diverse groups of organisms.

SYSTEMATICS

Any survey of the natural history of turritellines takes place against a backdrop of very inadequate systematic knowledge. The family Turritellidae (Table 1) appears to be a well-defined monophyletic group within the Cerithioidea (Houbrick, 1988), but its phylogenetic relationships with other cerithioid families remain unclear (Simone, 2001; Lydeard et al., 2002; Bandel, 2006). The most recent attempt at comprehensive systematic review of the family (Marwick, 1957a) divided Turritellidae into four subfamilies (Turritellinae, Protominae, Pareorinae, and Turritellopsinae), based almost exclusively on shell characters (see also Garrard [1972] for review of Australian species). A fifth subfamily, Orectospirinae, was proposed by Habe (1955) based on radular and opercular characters. Dall (1913) assigned the sessile, vermiform *Vermicularia*, which had been placed in Vermetidae, to its own family Vermiculariidae. Morton (1953) recognized Vermiculariinae as a subfamily within Turritellidae.

The reality of these subfamilial taxa as monophyletic groups, however, remains almost completely untested. It is, however, generally accepted that certain genera are *not* turritellines (e.g., *Mesalia* Gray, 1847 [see Squires & Saul, 2007]; *Tachyrhynchus* Mörch, 1868; *Turritellopsis* Sars, 1878; *Orectospira* Dall, 1925; and *Pareora* Marwick, 1931 [see Marwick, 1957a]), based mostly on shell characters but also on some anatomical data. These genera will therefore not be discussed further here. Several other genera (e.g., *Protoma* Baird, 1870; and *Zaria* Gray, 1847) are at least conchologically ambiguous. The single molecular phylogenetic study on the group (Lieberman et al., 1993) reveals that *Vermicularia* nests within other more conventional turritelline taxa, and this is consistent with data on soft anatomy (Morton, 1953; Hughes, 1985; Bieler & Hadfield, 1990); *Vermicularia* will therefore be considered as a turritelline here.

Based on this admittedly very incomplete understanding, the following discussion will be restricted to Turritellinae as listed in Table 1, keeping in mind that most of the genera/subgenera listed there are inadequately defined (reviewed by Allmon, 1996). Indeed, the genus *Turritella* has been called a "wastebasket" (Plotnick & Wagner, 2006) or "archetypal" (Nützel, 2005) genus because it is frequently applied uncritically, essentially as a "form genus" (*sensu* Sylvester-Bradley, 1954), to any turritelline-shaped gastropod shell. In the fossil record, turritellines are so widespread and abundant that the genus name "*Turritella*" is commonly used by geologists to designate not just most turritelline-shaped fossils, but also entire rock layers (see Allmon, 2007, for further discussion). This is despite the fact that it has long been widely accepted among systematists that the genus name *Turritella* Lamarck, 1799 (type species *Turritella terebra* (Linnaeus, 1758)) should not be applied to most of these species (Palmer, 1937; Marwick, 1957a). The species *T. terebra* itself is not well-known ecologically or systematically. A recent review of this species (Allmon et al., in review) has clarified its identify, geographic distribution, and aspects of its morphology, but the implications of these results for genus-level systematics remain to be explored fully.

The family Turritellidae was long reported to have originated in the late Paleozoic (e.g., Knight et al., 1960: 316; Sepkoski, 1982: 28), and the genus *Turritella* is still occasionally cited from the pre-Cretaceous (e.g., Fursich, 1984). Bandel (2006: 94) recently stated that "Turritellidae in a shell coquina are present from mid Jurassic onwards" … in the Middle Jurassic of Madagascar, but gave no details. In a personal communication (6/11/11) he clarified that this statement needs to be confirmed by new collections. It now seems clear, however, that the oldest definite representatives of the subfamily Turritellinae as discussed herein (and perhaps the family as well) are from the Early Cretaceous (Valanginian Stage) of France and Poland (Bandel, 1993; Tracey et al., 1993; Schröder, 1995; Kaim, 2004).

ABIOTIC ENVIRONMENT

Depth

Living turritelline species generally inhabit depths of 10–100 m, but a number of species live either in very shallow water (< 10 m) or in very deep water (> 200 m) (Allmon, 1988). For example, *Turritella cingulata* G. B. Sowerby I, 1825, in Chile, *Maoricolpus roseus* (Quoy & Gaimard, 1834) in New Zealand, and *T. duplicata* (Linnaeus, 1758) in Thailand occur regularly in the intertidal zone (Allmon, 1988, pers. obs; R. Waite, pers. comm.), and *T. gonostoma* Valenciennes, 1849, in the Gulf of California has been observed frequently in water less than two meters deep (Allmon, 1988; Allmon et al., 1992). Several species, on the other hand, (e.g., *Colpospira (Acutospira) smithiana* (Donald, 1900) and *C. (A.) yarramundi* Garrard, 1972, in Australia; and *T. yucatecanum* (Dall, 1881) in the Caribbean) occur at depths exceeding 500 m; *C. (Ctenocolpus) curialis* (Hedley, 1907) in Australia) apparently normally inhabit depths as great as 1,200–1,500 m (Allmon, 1988, and references therein). Although adequate data are not available for many species, it appears that at least some are able to live across a range of depths; *M. roseus*, for example, has been reported alive from depths from intertidal to > 200 m (Gunasekera et al., 2005).

Temperature

Turritellines were formerly treated by many authors as a typically "warm-water" group (Merriam, 1941), but this was based almost completely on their higher modern species diversity in lower latitudes, particularly in the southwestern Pacific (Allmon, 1988; Hendy & Allmon, 2007). Actual temperature measurements for living species show that a few do occur regularly in temperatures above 20°C (e.g., *Turritella variegata*; Bandel & Wedler, 1987), but these appear to be exceptions rather than representative of the group as a whole; most species actually prefer relatively cool water temperatures (< 20°C) (Allmon, 1988). Several recent authors have, in fact, treated fossil turritellines as typical of "cold" waters (Majima, 1985: 116; Kanazawa, 1990; Kim et al., 1999; Kitamura et al., 2000; Abdelhady, 2008).

It is also now clear that the temperature tolerance/preference of the group has changed (from warmer to cooler) during its history. This conclusion is based on (1) the occurrence of high abundances of turritellines in carbonate sedimentary environments only in the Cretaceous and Paleogene (Allmon, 2007), and (2) oxygen isotope paleothermometry of individual fossil turritellines from these ages indicate that they thrived in considerably warmer temperatures than they do today (e.g., Middle Eocene of the U.S. Gulf Coastal Plain – 19°C winter and 27–28°C summer [Andreasson & Schmitz, 2000]; mid-Paleocene of Denmark – 23.4°C winter and 28.5°C summer and [Thompson, 2000]).

Salinity

Merriam (1941: 10) stated that turritellines are animals of normal marine salinities and cannot tolerate brackish and estuarine environments. This appears to be the case for most living and fossil species (Allmon, 1988), but at least some living species appear to thrive under less-than-full-marine salinity. Around the British Isles, for example, Shumway (1979) found that *Turritella communis* Risso, 1826, was tolerant of salinity as low as 65% seawater (ca. 24 ppt), and Avens & Sleigh (1965) found that the same species remained active at salinities as low as 50% seawater (ca. 18 ppt). In waters around Hong Kong, turritellines (listed as either *T. terebra* (Linnaeus, 1758), or *T. bacillum* Kiener, 1843) have been frequently reported as abundant (Wu & Richards, 1981; Hickman, 1983; Shin, 1983; Taylor, 1994; Leung & Morton, 2003; Shenzhen Port Tonggu Channel Developing Office, 2003). These waters are heavily influenced by freshwater input from the Pearl River, which is the second largest in China, and regularly have salinities well below 30 ppt, especially in the summer because of increased runoff associated with the southwestern monsoon (Wu & Richards, 1981; Larsen et al., 2005). Similarly, Blay & Dongdem (1996) reported abundant occurrence (44/m^2) of *T. annulata* Kiener, 1843, in a coastal lagoon in Ghana, West Africa, at salinities as low as 12–15 ppt. Several fossil turritelline occurrences have also been interpreted as representing brackish, estuarine, or variable-salinity conditions (Funder et al., 2002; Latal et al., 2006; Naughton et al., 2007).

Nutrients

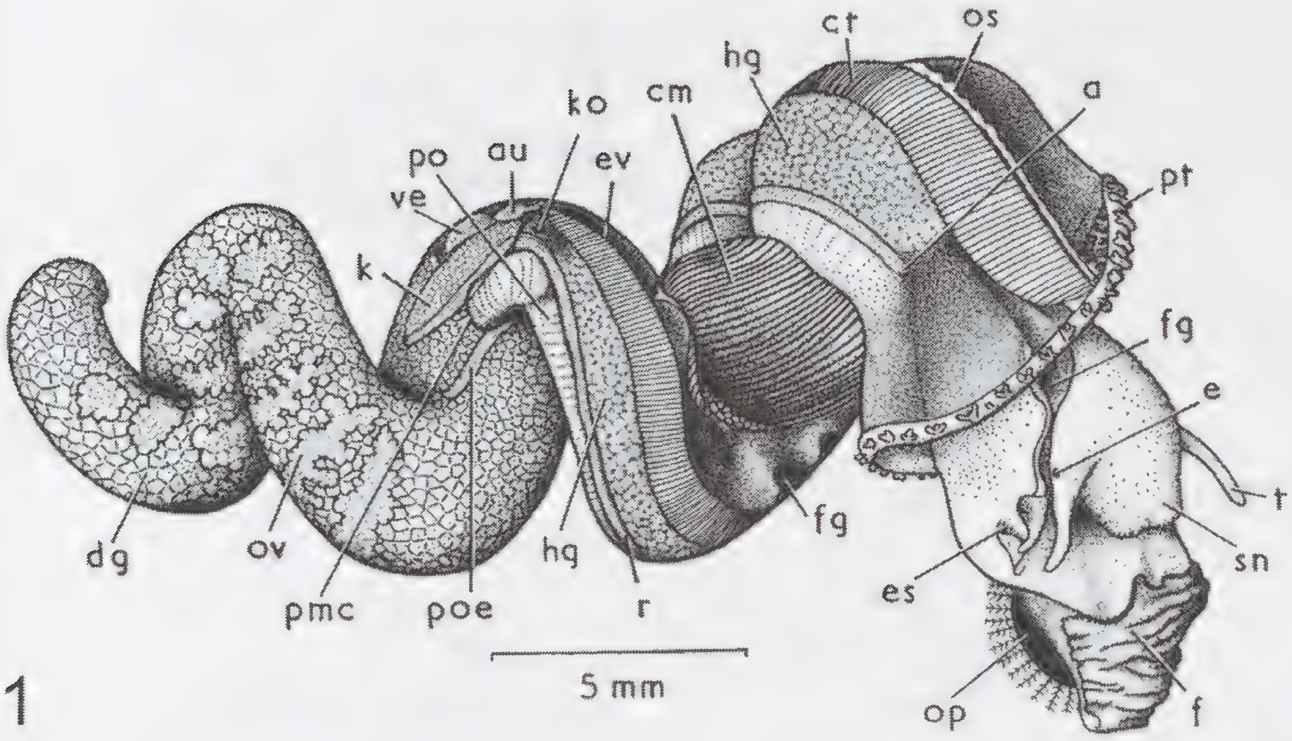
Although few direct measurements are available, a variety of proxy and circumstantial evidence supports the conclusion that high abundance in living turritellines is coincident with high levels of nutrients and primary productivity (Allmon, 1988; Allmon et al., 1992, 1994). This evidence can be grouped into at least three categories: (1) turritelline-dominated assemblages frequently occur in or near areas of moderate to high upwelling or terrestrial runoff (e.g., New Zealand, northern Gulf of California, Chile, west Africa, northern Venezuela, Hong Kong); (2) turritellines are rare or absent in modern oligotrophic, warm-water marine environments; and (3) turritellines are mainly suspension feeders and so would likely benefit directly from higher levels of planktonic productivity. For example, turritellines are relatively abundant in areas of the modern Adriatic in which nutrients are relatively high, and rare or absent where they are low (McKinney, 2003). Living turritellines are extremely rare on Pacific atolls, but are relatively abundant on Tarawa (Paulay, 1997, 2000), which is located in in the nutrient-rich waters of the equatorial upwelling zone, providing for much higher levels of productivity than typical of Oceania (Kimmerer & Walsh, 1981; Kimmerer, 1995; Paulay, 1997; Paulay & Kerr, 2001).

ANATOMY

Soft Parts

Soft-part anatomy is known in detail for only one turritelline species: *Turritella communis* from the northeastern Atlantic (Randles, 1900, 1902; Graham, 1938; Yonge, 1946; Johansson, 1946; Fretter & Graham, 1962, 1981; Kennedy, 1995). Less comprehensive information is available for a few other species: *Gazameda gunnii* (Reeve, 1849) from Australia (Carrick, 1980a, b); *Maoricolpus roseus* from New Zealand and Australia (Allmon et al., 1994; Bax et al., 2003); *T. gonostoma* from the Gulf of California (Allmon, 1988; Allmon et al., 1992); *T. terebra* from Hong Kong (Hickman, 1983); *T. banksi* Reeve, 1849, from Panama (Allmon, unpublished observations); *Vermicularia spirata* Philippi, 1836 (Morton, 1953; Bieler & Hadfield, 1990); and *V. pellucida* Broderip & Sowerby, 1829 (Hughes, 1985; Healy & Wells, 1998) (Figs. 1–11.) The description below is based on these sources.

The head-foot has a short, wide snout, and a pair of long cephalic tentacles, each with an eye situated near the base. The foot itself is relatively small, with a ciliated groove on the right side. The operculum is round, multispiral, and flexible, and usually bears peripheral bristles, except in *Vermicularia* (Morton, 1953).



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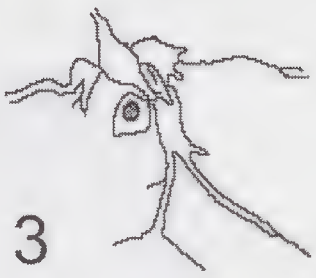

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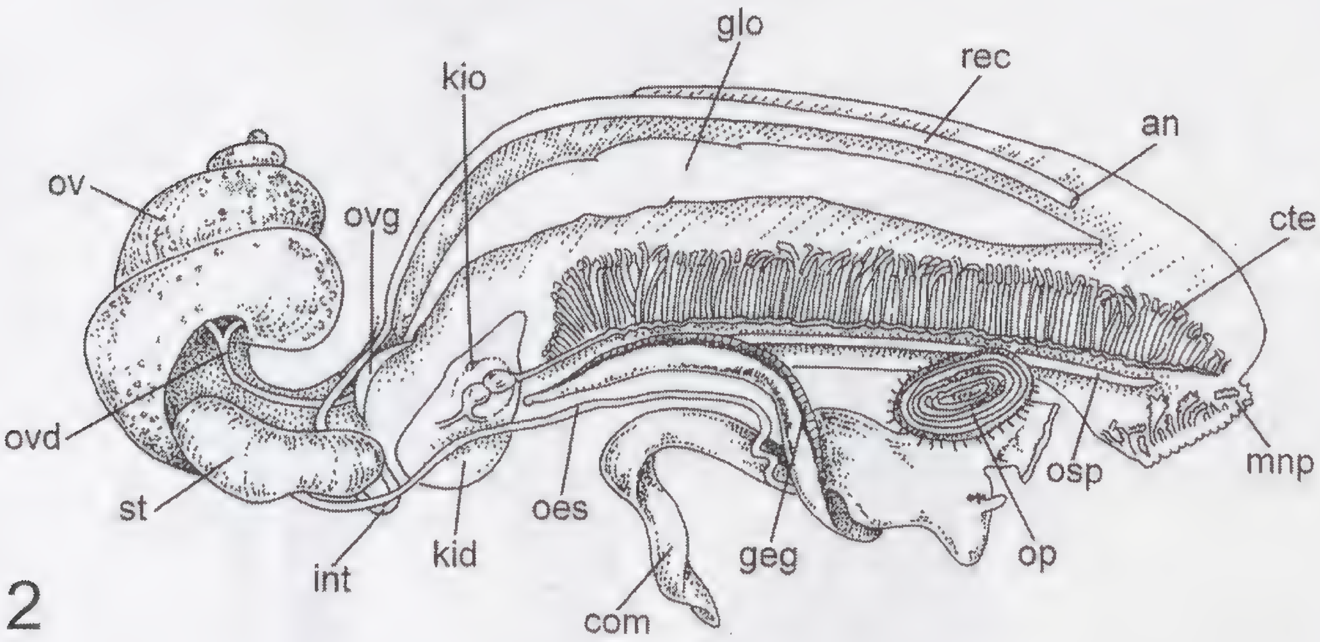

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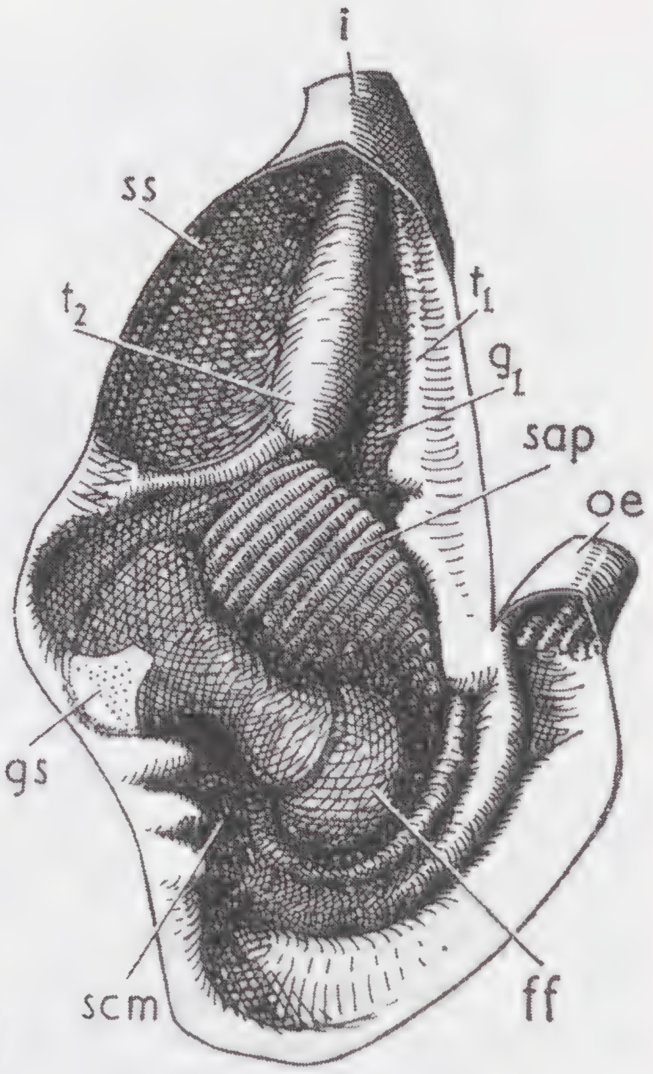

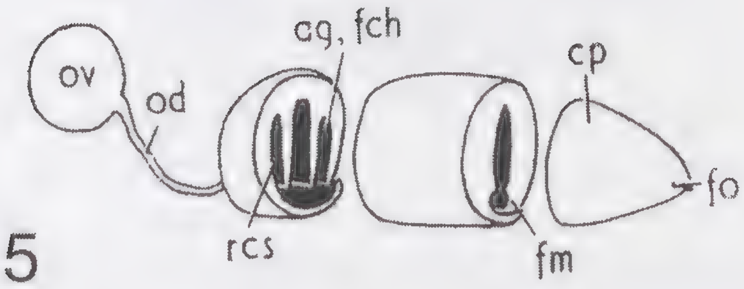

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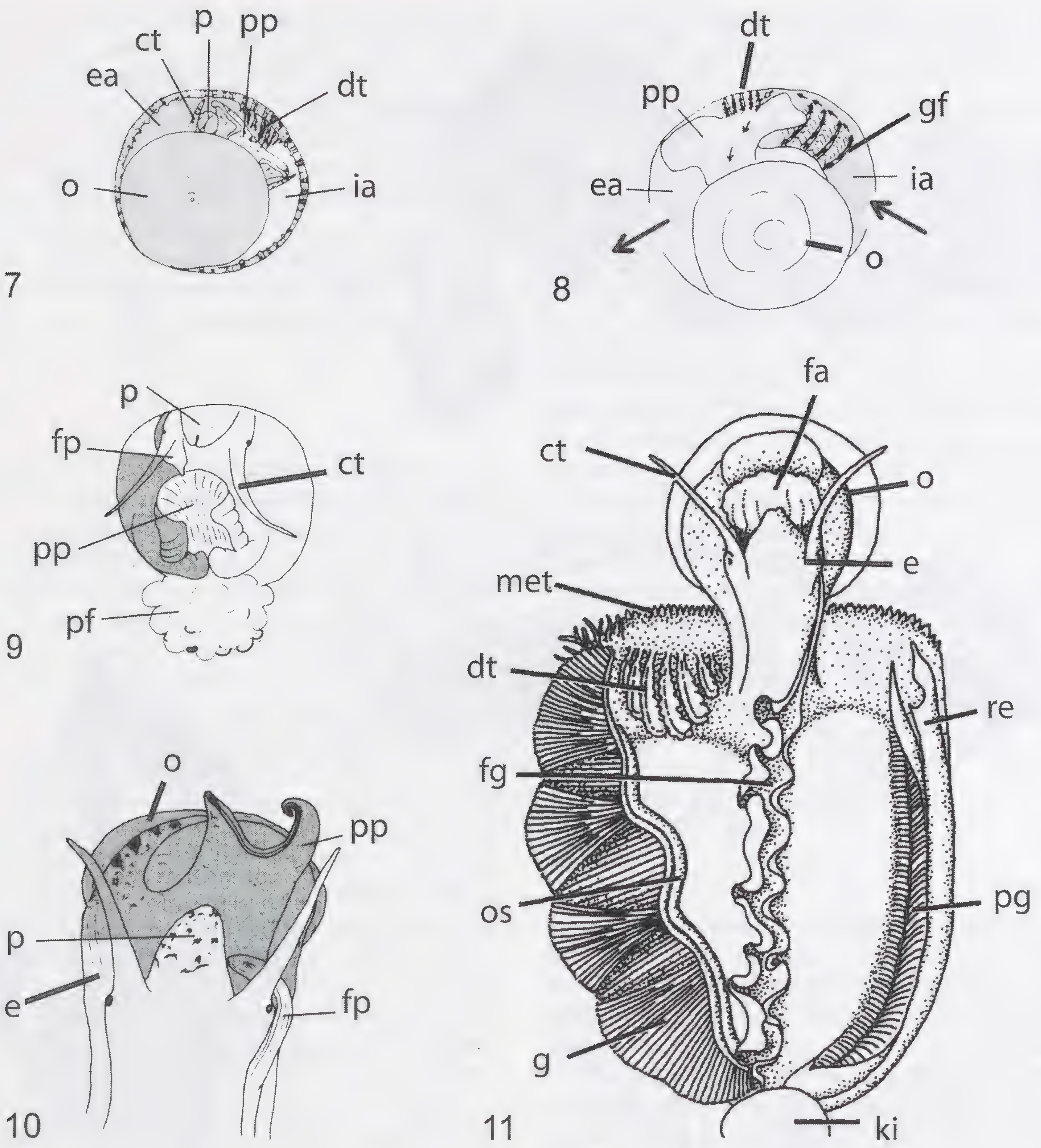
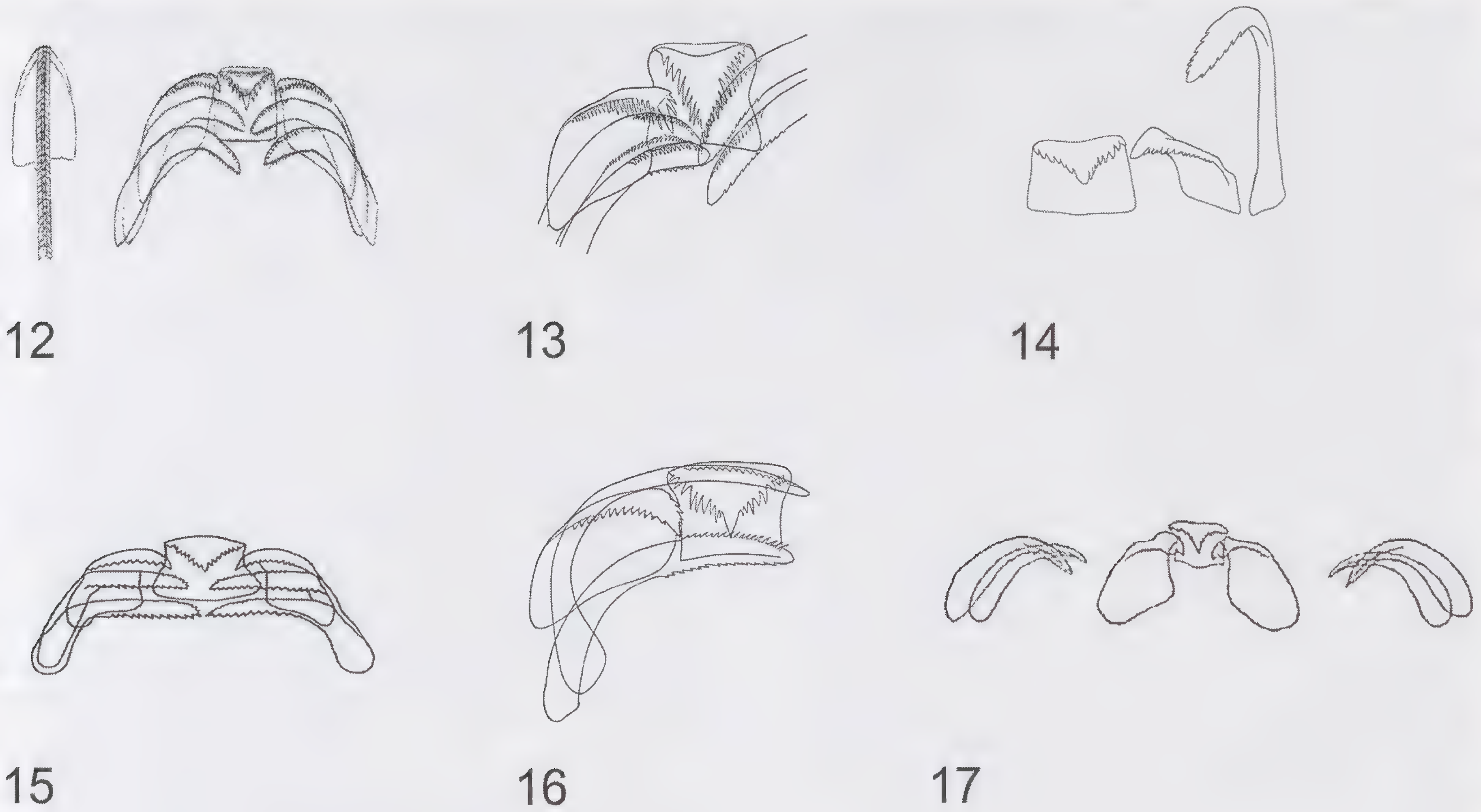
FIGS. 1–6. Soft-part anatomy of *Turritella communis*. FIG. 1: Entire animal, extracted from its shell (a = anus, au = auricle, cm = columellar muscle, ct = ctenidium, dg = digestive gland, e = eye, es = exhalent siphon, f = foot, fg = food groove, hg = hypobranchial gland, k = kidney, op = operculum, os = osphradium, ov = ovary, pmc = posterior limit of mantle cavity, po = pallial oviduct, poe = posterior esophagus, pt = pallial tentacles, r = rectum, sn = snout, t = tentacle, ve = ventricle) (modified from Fretter & Graham, 1962, fig. 57); FIG. 2: Anatomy of a female of *T. communis* with the mantle cavity opened, at approximately the same scale as FIG. 1 (an = anus, com = columellar muscle, cte = ctenidium, geg = genital groove, glo = glandular portion of oviduct, int = intestine, kid = kidney, kio = kidney opening, mnp = mantle papillae, oes = esophagus, op = operculum, osp = osphradium, ov = ovary, ovd = oviduct, ovg = oviducal gland, rec = rectum, st = stomach) (from Healy & Wells, 1998, after Randles, 1900); FIG. 3: Sketch of a portion of the nervous system, including an otocyst (*ot*) (modified from Randles, 1900); FIG. 4: Sketch of the nervous system, seen from above (modified from Randles, 1900); FIG. 5: Female genital duct. (ag = albumin gland, cp = capsule gland, fch = fertilization chamber, fo = genital duct opening, od = oviduct, ov = ovary) (from Fretter & Graham, 1962: fig. 186); FIG. 6: Stomach (dd = opening of duct of digestive gland, ff = fold emerging from spiral caecum, g1 = intestinal groove, gs = gastric shield, i = intestine, oa = esophageal aperture, sap = sorting area, scm = spiral caecum, ss = style sac region, t1 = major typhlosole, t2 = minor typhlosole) (from Fretter & Graham, 1962: fig. 121C).



FIGS. 7–11. Soft-part anatomy of *Vermicularia spirata*. FIG. 7: View looking into the aperture, showing operculum and pappilated margin of the mantle cavity; FIG. 8: Same view, showing movement of particles and mucus over the ctenidial filaments and onto the sole of the foot, where they accumulate as pseudofeces. Arrows indicate direction of water movement; FIG. 9: Pseudofeces collecting between the sole of the foot and the opercular rim; FIG. 10: Dorsal view of head, showing proboscis, propodium, food groove papilla, and operculum; FIG. 11: Female of *V. spirata*, with the mantle cavity opened, showing the pallial gonoduct. Abbreviations: ct = cephalic tentacle, dt = dorsal pallial tentacle, e = eye, ea = excurrent aperture, f = foot, fg = food groove, fo = foot, fp = food groove papilla, g = ctenidium; gf = ctenidial filament, ia = incurrent aperture, ki = kidney, met = mantle-edge tentacle, o = operculum, os = osphradium, p = proboscis, pp = propodium, pf = pseudofeces, pg = pallial gonoduct, re = rectum. FIGS. 7–10 modified from Hughes, 1985; FIG. 11 modified from Bieler & Hadfield, 1990.

The mantle cavity is elongated, and divided into two compartments by the attachment of the mantle to the cephalopedal mass in the middle of the animal's dorsum. The entrance to the mantle cavity, on the animal's left, is surrounded by rows of papillae or tentacles, which prevent the entrance of large particles. Inside the larger left compartment of the mantle cavity, smaller particles in the incurrent stream are caught on the single elongate ctenidium. The

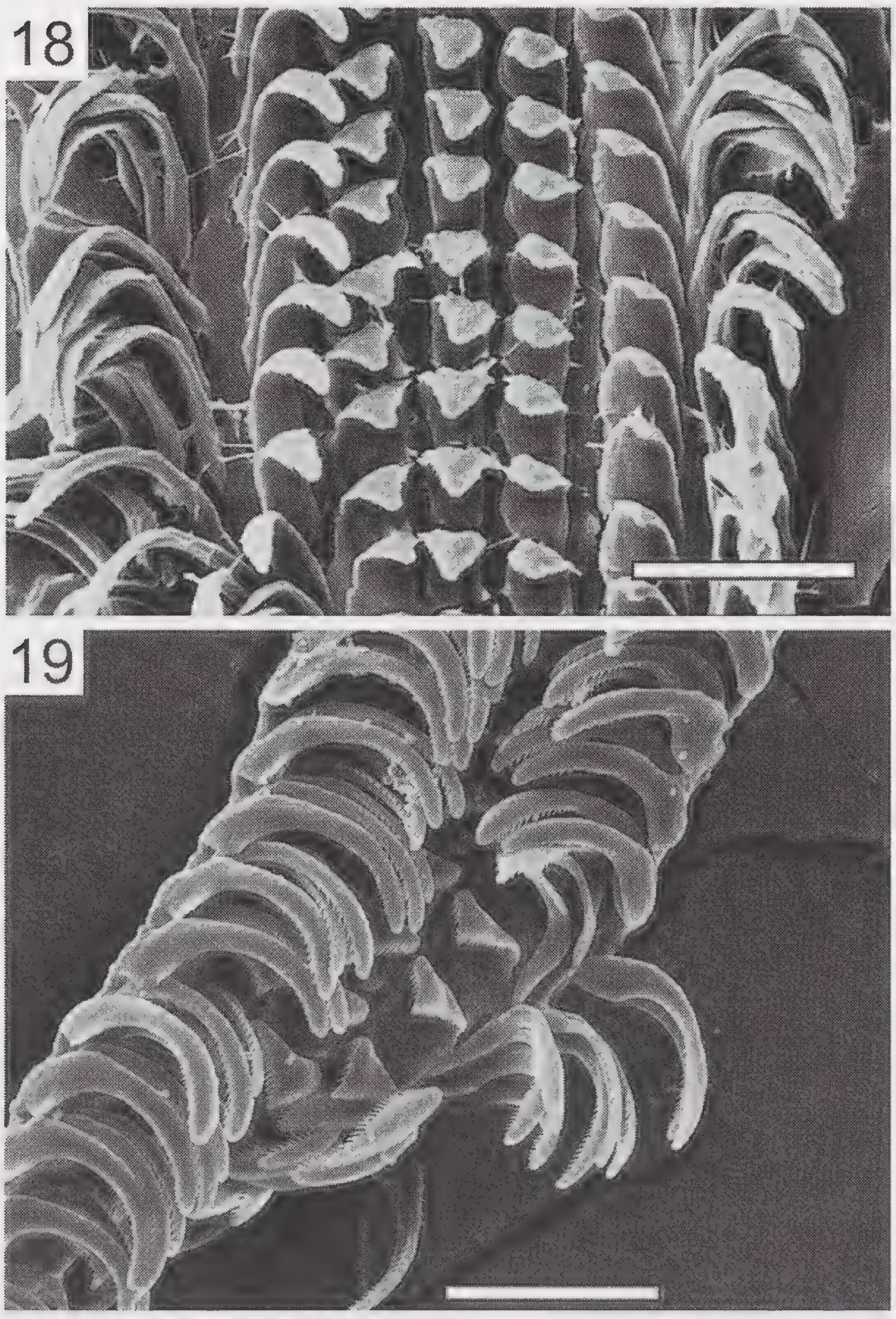


FIGS. 12–17. Previous drawings of turritelline radulae. FIG. 12: *T. communis* from Sars (1878); FIG. 13: *T. communis* from Morton (1953); FIG. 14: *T. communis* from Bandel (1984); FIG. 15: *T. spectrum* Reeve, 1849 (=? *T. terebra*) redrawn from a drawing associated with specimen in the collection of the Academy of Natural Sciences, ANSP 38621; FIG. 16: *Vermicularia spirata* from Morton, 1953; FIG. 17: *Colpospira (Ctenocolpus) australis* (Lamarck, 1822) modified from Randles, 1900.

ctenidial filaments are narrow, elongated, and laterally flattened. Each filament is attached to the ctenidial axis by its base and fixed to the adjacent mantle skirt on the right of the axis by the basal third of its dorsal surface. In this way, the long axes of the filaments lie roughly parallel with the roof of the mantle cavity and their tips curve over to rest on the floor. Captured food particles are passed by ciliary action to the tips of the gill filaments, which then convey them into a deep groove in the mantle floor. There the particles are trapped in a mucous strand or rope secreted by a combination of the hypobranchial gland, a strip of cells ("confusingly termed" [Hughes, 1985: 323] the "endostyle") along the ctenidial axis, and by the gill filaments and the walls of the groove. In this food groove, the mucous strand is constantly rotated and eventually reaches a peripheral spoon-shaped fold into which the animal extends its radula to gather the accumulated food. Inside the mouth is a pair of thin, weak jaws.

Surprisingly little has been published about turritelline radulae since the brief descriptions of Cooke (1895) and Randles (1900). Cooke noted that the turritelline radula is small and taenioglossate; that is, characterized by seven teeth per row, including a "central tooth of very variable form, the prevailing type being multicuspid, the central cusp the largest, on a rather broad base; a single lateral, which is often a broad plate, more or less cusped, and two uncini [marginal teeth], rather narrow, with single hooks, or slightly cusped" (1895: 223). Cooke also remarked on the turritelline radula's relatively small size, an observation repeated by Graham (1938: 458–459) for *Turritella communis*. Graham noted that a "generally simple and reduced radula bearing fine teeth" would be consistent with the species' presumed exclusively suspension-feeding habit, and is "most frequently used for raking in the mixture of food and lubricating material brought to the mouth ready mixed along the ciliated groove and not for the independent collection of food". Carrick (1980a, b) similarly noted that the radula in *G. gunnii* is reduced relative to other cerithioids, but also that it does show patterns of wear that apparently reflect rasping against the larger sediment particles entrained by the mucus rope.

Randles noted that "there is a considerable amount of variation in the radulae of different species" of turritellines (1900: 58; Figs. 12–17). All species for which data are available have a single median or rachidian tooth, and a single lateral tooth and two marginal teeth to each side (i.e., 2 + 1 + 1 + 1 + 2 formula) (Figs. 12–19). Boss (1982) and Healy & Wells (1998), however, stated (without providing specific sources) that the number of marginals varies from zero to three within the family (this information may have originated with Troschel [1856] [R. Bieler, pers. comm., March 2011]). The rachidian tooth is quadrangular in shape, with a relatively broad, straight base and a reflexed triangular apex, the margin of which bears a large central cusp bordered laterally by numerous smaller denticles. The lateral teeth have finely denticulate free margins, and vary in size from approximately equal to considerably larger than the rachidian. The marginals are sickle- or scythe-shaped, their edges "being serrated in such a manner as to impart a feathery appearance to the tooth when that is turned over and seen in surface view" (Randles, 1900: 58).



FIGS. 18–19. Scanning electron micrographs of turritelline radulae. FIG. 18: *Turritella nzimaorum* Ryall and Vos, 2010, from Ghana. Scale bar = 50 μm (from Ryall and Vos, 2010); FIG. 19: Previously unpublished image of the radula of *Turritella trisulcata* Lamarck, 1822, from the Red Sea. Scale bar = 50 μm (specimen in the collection of the Paleontological Research Institution).

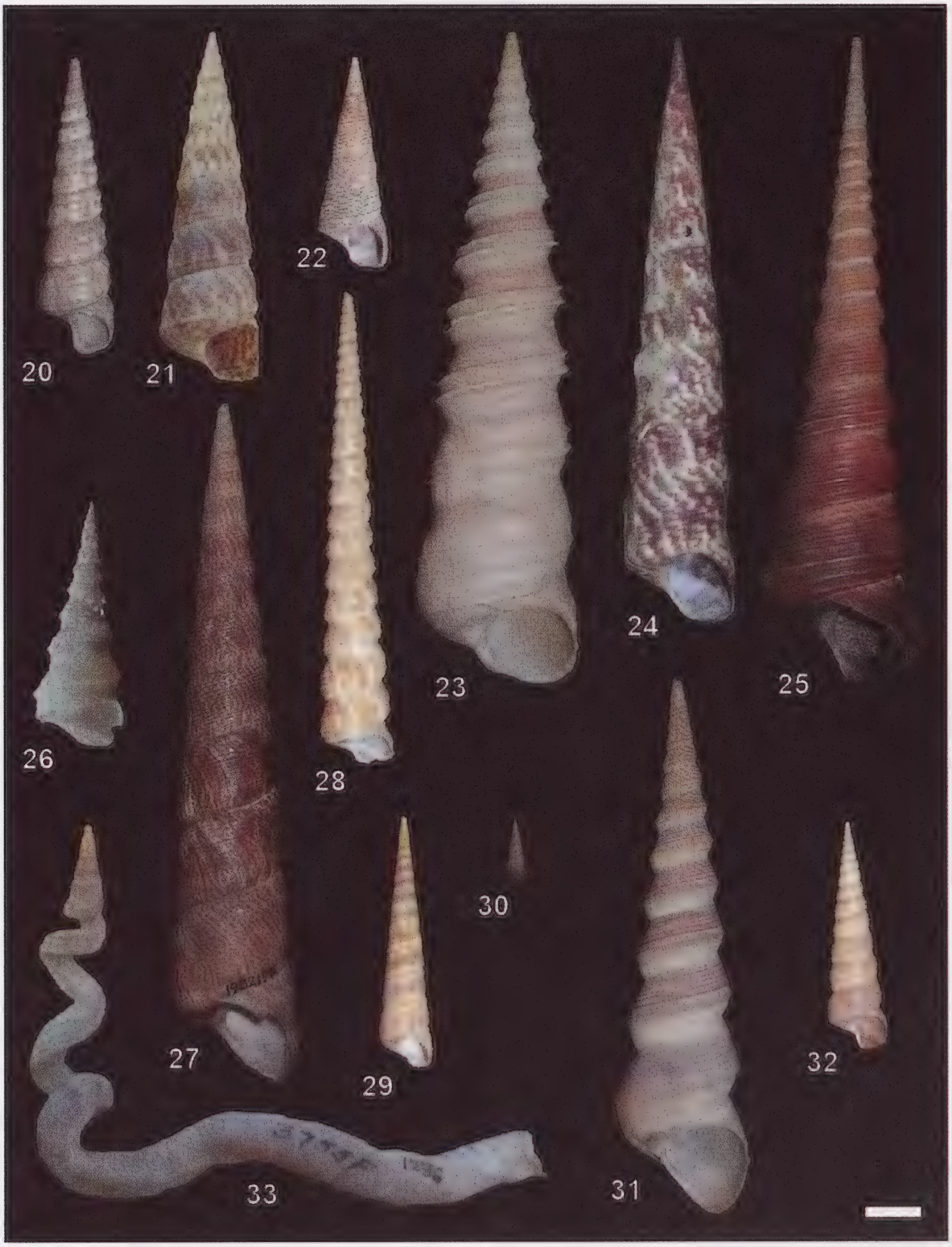
Scanning electron micrographs of turritelline radulae have only recently become available (Figs. 18, 19). These images confirm most earlier observations. The radular ribbons are indeed very small, measuring approximately 150 μm wide. The rachidian and lateral teeth are of approximately equal size and are finely denticulate, and the marginals are narrow and elongate, and finely-denticulate.

The esophagus is a straight tube with a dorsal food channel (A. Graham, 1939). It leads to a relatively complex stomach (Seshaiya, 1932; Fretter & Graham, 1962; Fig. 6). A gastric shield covers much of the stomach wall, and a crystalline style abuts the shield. (The crystalline style – a stiff rod of mucoprotein which, as it rotates and dissolves in the stomach, dissolves and releases digestive enzymes – is present in almost all bivalves and most suspension feeding gastropods [Yonge & Thompson, 1976; Purchon, 1977; Hughes, 1986; DeClerck, 1995].) An area of folds on the stomach wall acts as a sorting area for the food particles.

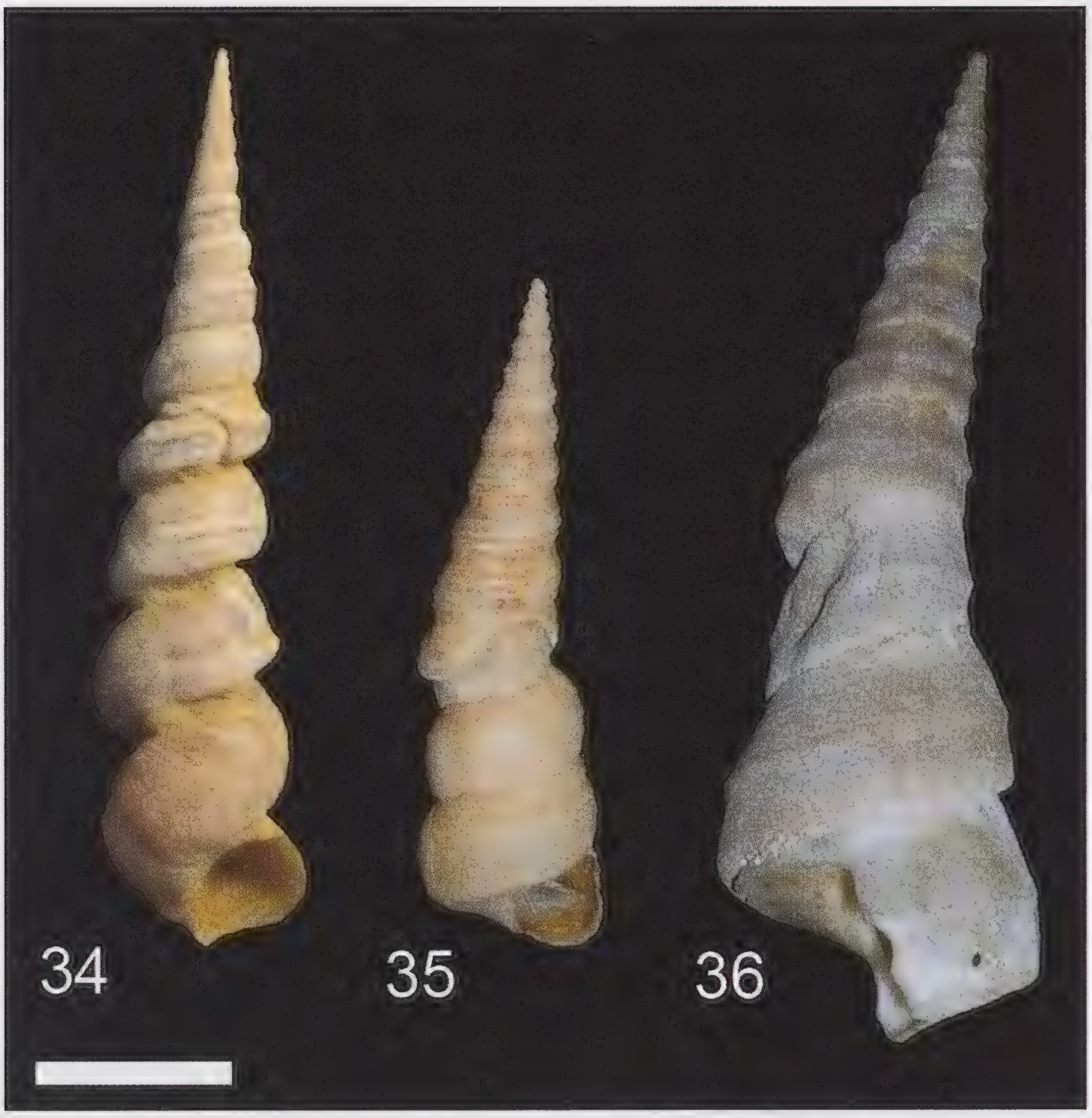
The high spire of the turritelline shell is filled almost to the apex with a tightly-packed visceral mass, consisting of two closely-appressed organs, an elongated digestive gland and an elongated gonad (Figs. 1, 2).

Water currents exit the mantle cavity on the right side of the animal via an excurrent siphon formed by folds of the mantle edge. The stream exiting this siphon is strengthened by the action of cilia over the rectum and the open pallial genital duct, so that the ovoid fecal pellets of compacted particles are expelled clear of the animal's head. Their expulsion is usually reinforced by a slight but sudden retraction of the head-foot into the mantle cavity.

Both male and female reproductive tracts have coelomic and pallial (mantle cavity) sections. There is no copulatory organ. In males, sperm is delivered from the gonad in a seminal duct, a part of which is altered into an open prostate gland. From here the sperm duct narrows and runs into the floor of the mantle cavity along a folded, ciliated groove between the right fold of the food groove and the excurrent "pseudo-siphonal process". In females (Figs. 2, 6), the coelomic oviduct leads into the hind part of the mantle cavity, which contains a developed pallial oviduct divided into medial and lateral laminae. Two pouches, a receptaculum seminis and a bursa fertilization/albumen chamber, lie on either side of the



FIGS. 20–33. Adult shells of some living turritelline species, selected to represent the group's present range of morphological variation. Scale bar = 1 cm. FIG. 20: *Turritella bicingulata* Lamarck, 1822, Azores, Natural History Museum, London (NHM) Collection; FIG. 21: *T. variegata* (Linnaeus, 1758), Venezuela, Paleontological Research Institution (PRI) Collection; FIG. 22: *Maoricolpus roseus* (Quoy & Gaimard, 1834), New Zealand, NHM Collection; FIG. 23: *T. duplicata* (Linnaeus, 1758), India, NHM Collection; FIG. 24: *T. gonostoma* Valenciennes, 1832, Peru, NHM Collection; FIG. 25: *T. terebra* (Linnaeus, 1758), Philippines, NHM Collection; FIG. 26: *T. carinifera* Lamarck, 1822, South Africa, PRI Collection; FIG. 27: *T. broderipiana* d'Orbigny, 1840, Peru, NMH Collection; FIG. 28: *T. columnaris* Kiener, 1834, Somalia, NHM Collection; FIG. 29: *Gazameda gunnii* (Reeve, 1849), Australia, NHM Collection; FIG. 30: *Stiracolpus delli* Marwick, 1957, New Zealand, NHM Collection; FIG. 31: *T. accutangula* Linnaeus, 1758, Malaysia, NHM Collection; FIG. 32: *T. communis* Risso, 1826, English Channel, NHM Collection; FIG. 33: *Vermicularia fargoi* Olsson, 1951, Florida, PRI Collection. (Photos from NHM Collection courtesy of Ursula Smith).



FIGS. 34–36. Modern turritelline shells showing aberrant morphologies following shell breakage. FIG. 34: *Turritella communis*, Adriatic Sea, PRI Collection; FIG. 35: *T. communis*, Isles of Scilly, Cornwall, England, NHM Collection; FIG. 36: *T. carinifera*, South Africa, NHM Collection. Scale bar = 1 cm.

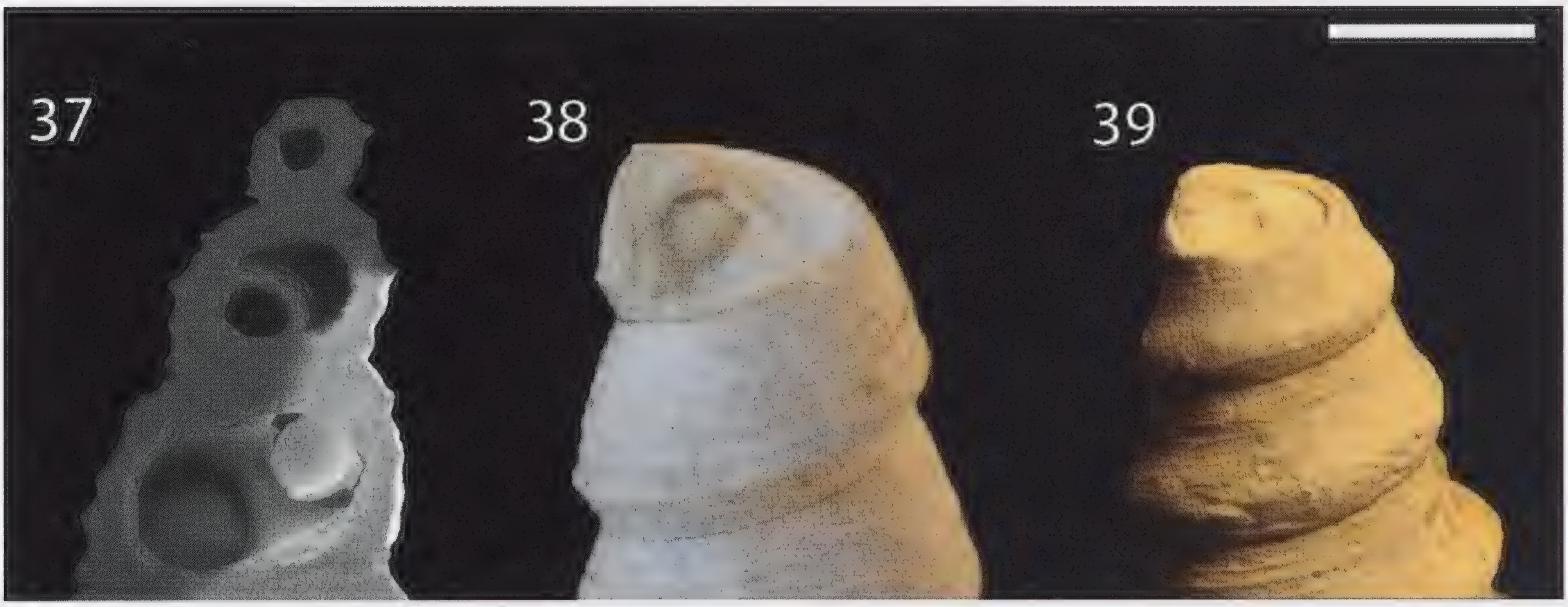
posterior pallial oviduct. A large pallial capsule gland completes the encapsulation of fertilized eggs and albumen during spawning. As is also the case for other related aphallate families (e.g., Cerithiidae, Melaniidae, Potamididae, Vermetidae), the pallial oviduct is open.

The nervous system is zygoneurous (Bouvier, 1887; Randles, 1900; Fig. 4), and has relatively long connectives between the cerebral ganglia, a subesophogeal ganglion close to the pleural ganglion, and short cerebropedal connectives (Randles, 1900). *Turritella communis* is reported to have "a single large circular otolith" (Fig. 3) (Randles, 1900: 63).

Shell

The turritelline shell (Figs. 20–33), as noted by Gould (1969: 433), has long been cited for the elegant mathematical regularity of its coiling (Moseley, 1838; Thompson, 1942). It consists of 15 to 30+ round to angulate whorls (see, e.g., whorl profile diagrams in Allmon, 1996), which succeed each other with high translation rate around the coiling axis, resulting in the characteristic high-spired "turritelliform" shape. The columella is usually indistinct. The aperture is not entire, and its inner surface bears only a slight callus. There is no discrete anterior siphonal notch.

Shell growth is indeterminate, but there are frequently signs of gerontism in the latest whorls of some species, especially slight to significant uncoiling (Pérez, 1929; Andrews, 1974). This is taken to the extreme in *Vermicularia*, which in most respects looks like a "normal" turritelline as a juvenile, but then begins to uncoil after 10–15 whorls (Gould, 1969; Hughes, 1985) and becomes completely, and usually permanently, sessile (Fig. 33). (Gould [1968] described a remarkable local population of *Vermicularia* in Bermuda, the majority of which do not uncoil



FIGS. 37–39. Apical infillings in Recent and fossil turritellines. FIG. 37: *Maoricolpus roseus*, Recent, New Zealand. Scanning electron micrograph of a longitudinal slice through the shell apex, showing three meniscate septae. Image courtesy of Ursula Smith; FIG. 38: *Turritella robusta*, Late Miocene, Panama, showing broken apex revealing meniscate septum; FIG. 39: *Kapalmerella mortoni*, Paleocene, Alabama, showing broken apex revealing amorphous infilling. Scale bars = 5 mm. All specimens in the PRI Collection.

at all as adults, but stay mostly buried in soft substratum as do other turritellines.) Uncoiling and other "abnormalities" of the turritelline shell are frequently associated with trauma (such as breakage associated with unsuccessful predation; see below) (Figs. 34–36).

Many living and fossil turritelline species show secondary internal structures in apical whorls, ranging from one or more meniscate septa to solid infillings or plugs, which seal the apex if it is broken off (decollation) (Tate, 1893; Boekschoten, 1967; Andrews, 1974; Figs. 37–39). Similar features are known in many other fossil and recent gastropod groups (Draper, 1985; Gubanov et al., 1995; Rohr & Measures, 2001). Despite their widespread occurrence, however, neither their function nor mode of formation is well understood.

At least one fossil species assigned to Turritellidae (although not necessarily to Turritellinae) shows the "agglutinating" habit – attaching shells and other objects to the outside of the shell – similar to the gastropod *Xenophora*. Shells of *Springvaleia leroyi* (Guppy, 1867) from the Late Miocene of Panama, Trinidad, and Venezuela show imprints of bivalve shells and other foreign objects on the external surface of the shell (Rutsch, 1942: 133; Weisbord, 1962: 150).

Despite their reputation for homogeneity, turritelline shells show considerable variation in shape and external sculpture (Figs. 20–33). Yet little is known about the functional morphology of these or other aspects of the turritelline

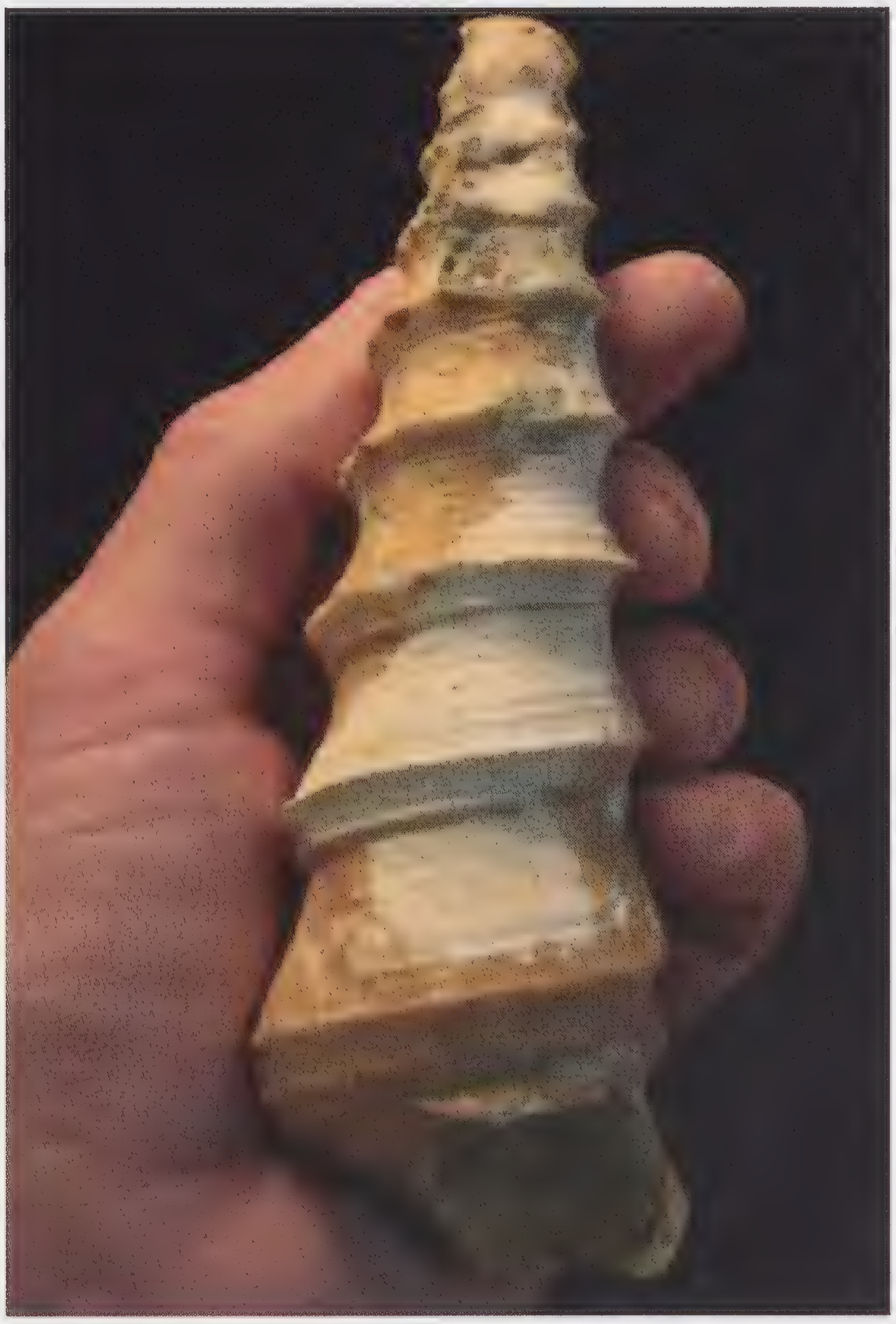


FIG. 40. A very large specimen of the largest known turritelline species: an unnumbered specimen of *Turritella robusta* in the collection of the Natural History Museum, Basel Switzerland, from the Late Miocene of the Darién region of Panama, locality 18529. Specimen is approximately 17 cm long.

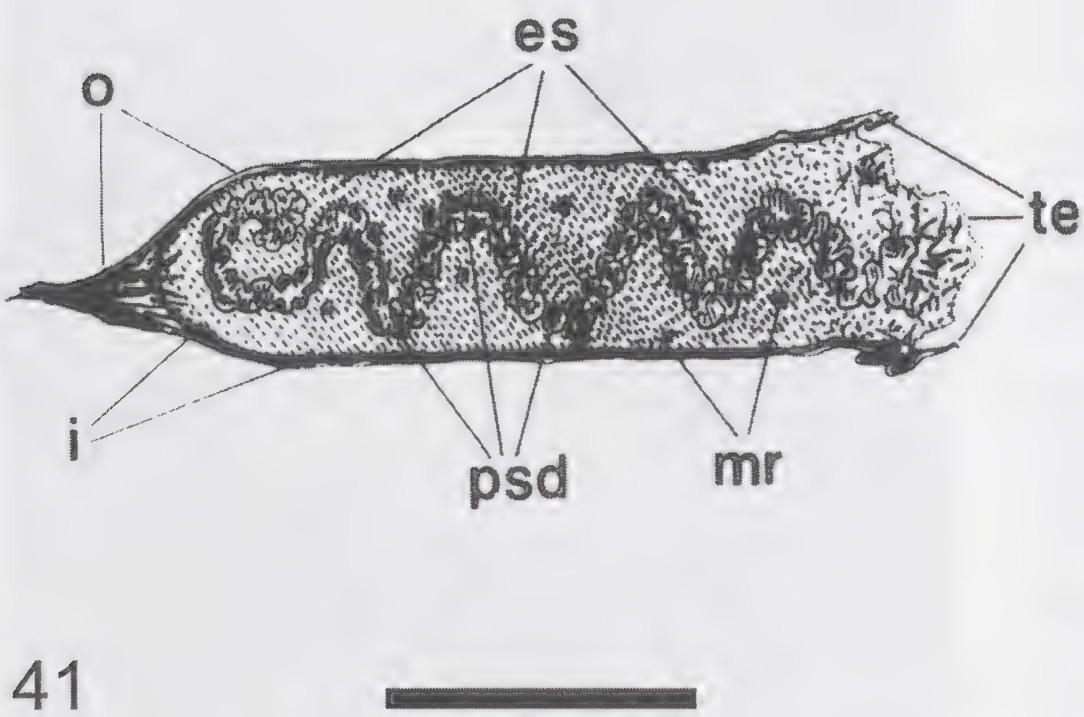
shell. Although some authors have argued that the turritelliform shell form itself may function to resist predation (by permitting deep withdrawal by the animal from the aperture) (Signor, 1985; Vermeij, 1987: 195, 220), there is no direct evidence of an anti-predatory function for any details of shell structure. Circumstantial evidence from fossils suggests that external sculpture does not have a significant anti-predatory function (Allmon et al., 1990), but this has not been tested experimentally in living species. The turritelliform shape is by definition largely isometric, but significant allometry is probably present in most species, suggesting that heterochrony may be an important evolutionary pattern in the group (Andrews, 1974; Allmon, 1994). The range of morphological variation of the shell has been examined in only two living species: *Turritella communis* (Wright, 1956; Charles, 1977), and *T. terebra* (Allmon, 1996).

Living species range from approximately 10 to 175 mm in complete adult shell length (e.g., Figs. 20–33), with most ranging from 30–100 mm. The smallest known turritellines are probably several species of Recent *Platycolpus* from Australia (Garrard, 1972). The largest known turritelline is the fossil species *Turritella robusta* Grzybowski, 1899, from the Miocene and Pliocene of Venezuela, Trinidad, and Panama, which reached lengths of more than 200 mm (Woodring, 1957: 107; Fig. 40).

REPRODUCTION AND EARLY ONTOGENY

General Reproductive Biology

In all but two of the living turritelline species for which information is available, sexes are separate; in all known species, males are aphallate, and fertilization is internal (Allmon, 1988; Bieler & Hadfield, 1990; Kennedy, 1995; Healy & Wells, 1998). The exceptions are the Australian turritelline *Gazameda gunnii,* and the uncoiled *Vermicularia spirata*, both of which are protandrous hermaphrodites in which all hatchlings are male. In *Gazameda*, these pass through an intermediate phase during which they have both male and female anatomical features, after which individuals become and remain fully female (Carrick, 1980a, b). In *Vermicularia*, the juvenile males are free-living, and become attached to the substratum and start to uncoil about the time they undergo sex change (Bieler & Hadfield, 1990). In the two species that have been studied in most detail – *Turritella communis* from the northeastern Atlantic and *Maoricolpus roseus* from New Zealand and Australia – as well as in *V. spirata*, females are larger than males (Pelseneer, 1926; Wright, 1956; Bieler & Hadfield, 1990; Kennedy, 1995). A similar pattern of sexual dimorphism has been hypothesized for several other living and some fossil turritellines (Kotaka, 1980). In *G. gunnii*, shells of females brooding



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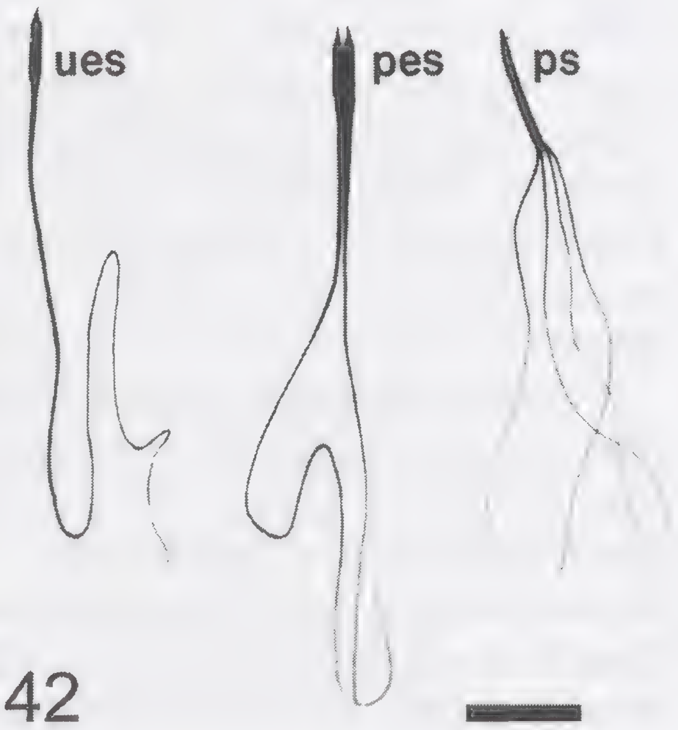

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FIGS. 41–42. *Turritella communis.* FIG. 41: Spermatophore (es = euspermatozoal mass; i = inner gelatinous wall; o = outer membranous spermatophore covering; psd = diverticular membrane containing paraspermatozoa; te = torn end of spermatophore). Scale bar = 1 mm (after Kennedy, 1995); FIG. 42: Unpaired euspermatozoon (ues), paired euspermatozoa (pes), and multiflagellate paraspermatozoon (ps). Scale bar = 10 µm (after Kennedy, 1995).

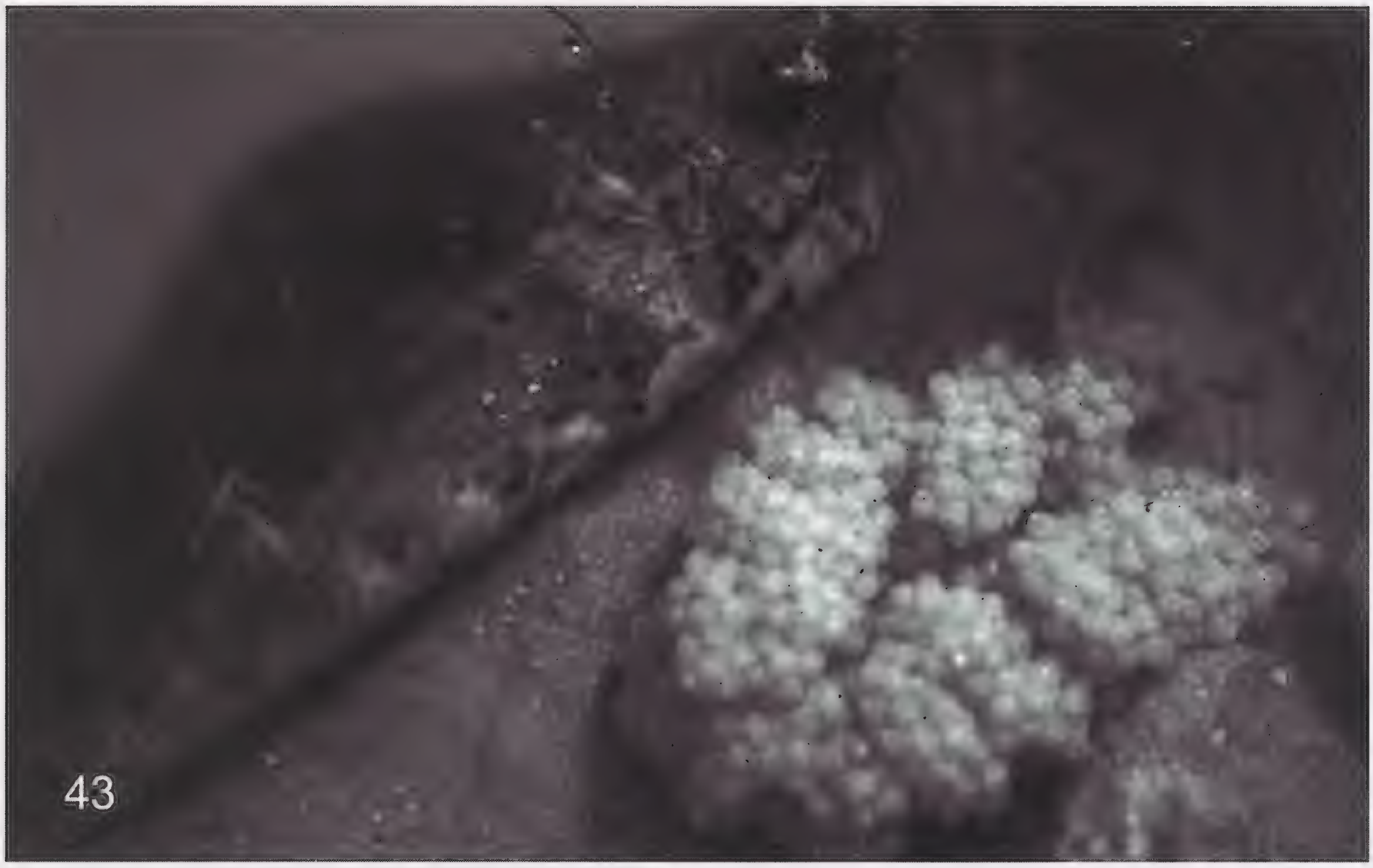
eggs or juveniles are larger and have more swollen later whorls than do males (Iredale, 1924; Merriam, 1941).

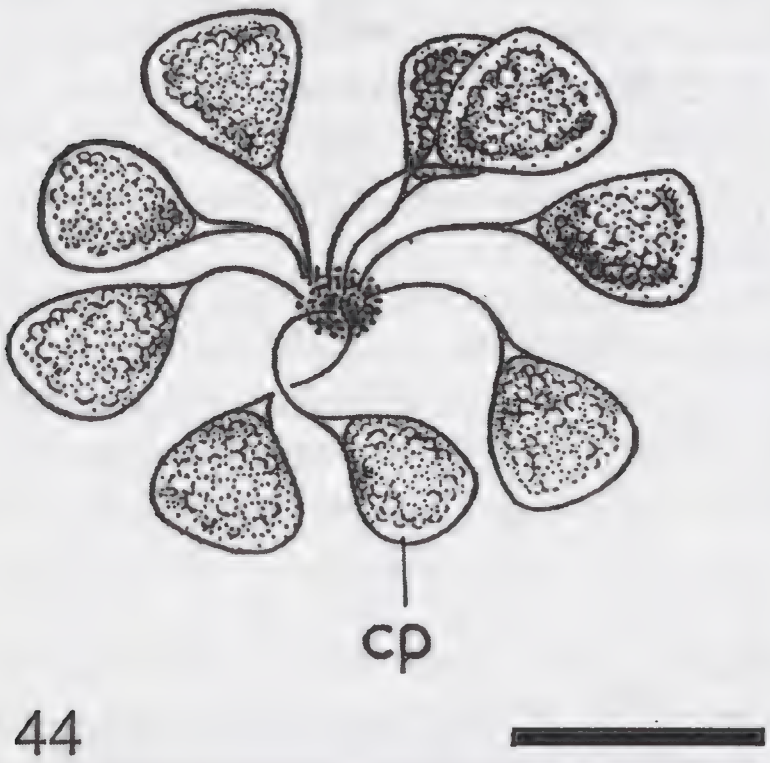
Although it has never been specifically reported, in most species sperm are assumed to be broadcast by the male into the water, and taken in by the female via her incurrent siphon (Fretter, 1953; Fretter & Graham, 1962: 361; Morton & Miller, 1968: 582). In *Turritella communis*, however, pseudocopulation (the close positioning, without intromission, of male and female to facilitate contact between eggs and sperm at the time of discharge [Thorson, 1950]), in which one or more males delivers one or more spermatophores directly to a single female, has been described in detail (Kennedy, 1995). Kennedy described "pseudocopulation groupings of 3–11 males in star-shaped arrangements" surrounding a female buried in the substratum. Males are presumably attracted by some kind of chemical signal emitted by the female, and "erupt from the sediment" and craw along the surface as far as 0.5 m to locate her. Males produce a "complex double-walled cylindrical spermatophore [3–4 mm in length; Fig. 41] containing paired and unpaired euspermatozoa, and multiflagellate paraspermatozoa" (Fig. 42). Kennedy reported that the spermatophore "is delivered to the hind part of the mantle cavity from the coelomic vas deferens and is moulded in a tight, spirally bound tubular form as it emanates on the right side of the head. A tract of forward beating cilia runs between the right fold of the food groove and the exhalent pseudo-siphonal process on the right side of the cephalopedal complex. Along this tract, the tube of sperm can be seen to steadily extrude by thrust and ciliary action towards the aperture opening. At this time the head-foot is stretched forward and out of the aperture…" (Kennedy, 1995: 428). Kennedy also found that smaller males were proportionately more active than larger males in sperm transfer, and that about 15% of males and 3% of females were synchronously fertile at the maximum observed level of reproductive activity.

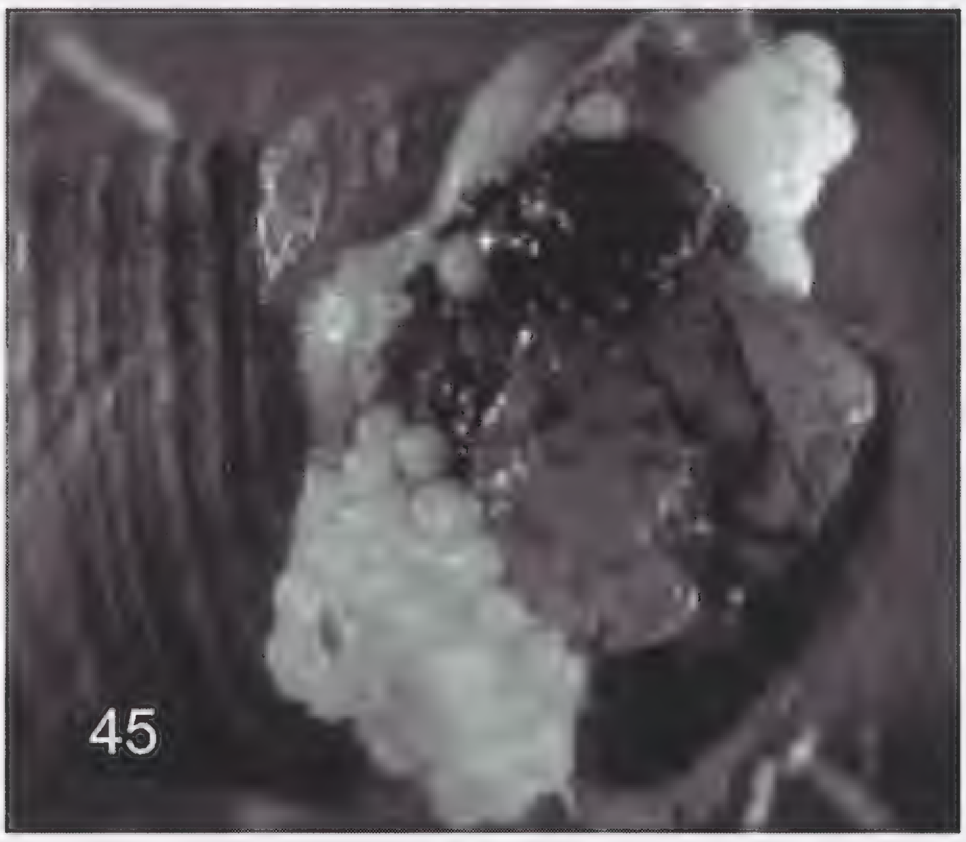
Fretter & Graham (1962: 361) suggested that in *Turritella communis*, "spawning of large numbers probably occurs simultaneously" (presumably meaning synchronous release of sperm by multiple males), but presented no definite evidence. In any case, several turritelline species certainly have "mass spawning" in the sense of many females laying eggs at one time: the confirmation by Kennedy (1995) of active aggregation of reproductive individuals of *T. communis* suggests that similar occurrences of high densities of similar-sized adults at times of reproduction in *T. gonostoma* Valenciennes, 1839, in the Gulf of California (Allmon, 1988; Allmon et al., 1992), *T. variegata* Linnaeus, 1758, in Venezuela (Bandel, 1975, 1976; Petuch, 1976), and *T. annulata* Kiener, 1843, in Ghana (Buchanan, 1958) may support similar interpretations. "Gregariousness," Kennedy concludes, "… appears to be a critically essential life strategy among these aphallic, internally fertilizing gastropods." (1995: 432) (see further discussion below). (As discussed by Gould & Robinson [1994: 371; following Hadfield & Hopper, 1980], because the common ancestor of all cerithioids was likely aphallate, this may have opened "evolutionary access to fertilization at a distance".)

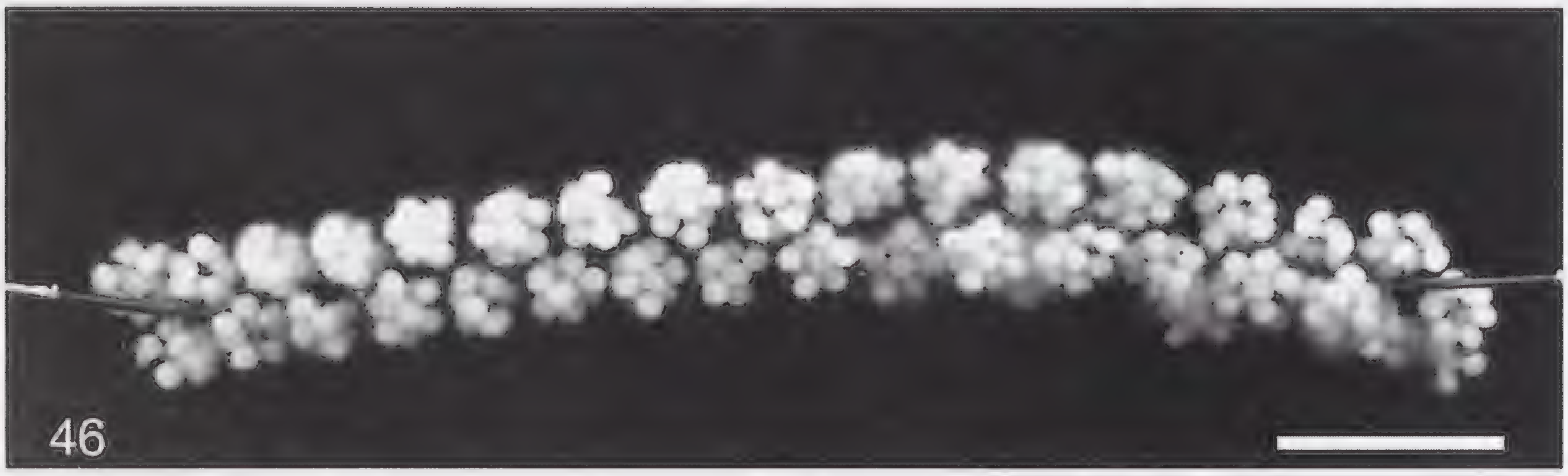
Eggs and/or egg capsules have been described for six living turritelline species (*Turritella communis* [Lebour, 1933; Fretter & Graham, 1962; Kennedy & Keegan, 1992]; *T. variegata* [Flores & Macsotay, 1972; Bandel, 1975, 1976]; *T. gonostoma* [Allmon et al., 1992]; *T. cingulata* [Romero et al., 2003]; *Maoricolpus roseus* [Bax et al., 2003]; and *Vermicularia spirata* [Bieler & Hadfield, 1990]) (Figs. 43–46). In *T. communis*, the pallial duct ends in two pouches (Fretter & Graham, 1962; Figs. 2, 5); one serves as a receptaculum seminis, and sperm reach it through the mantle cavity by swimming against ciliary currents; the other pouch appears to be the location of fertilization of the eggs. After fertilization the eggs are packaged into capsules, consisting of up to 300 (for most species < 50) eggs embedded in albumen and surrounded by a wall which is secreted as the spawn mass passes out of the pallial duct. Hundreds to thousands of these capsules are then embedded in a mass of gelatinous matrix. The matrix is sticky, and the mass is usually covered with adhering sand grains or bound into a more fixed structure. The entire mass is usually unattached or only loosely attached to the substratum, and rolls along the bottom with currents. Development within the egg capsule lasts 7–18 days; generally the larger the egg size, the longer the intracapsular period (Romero et al., 2003). In both *M. roseus* and *V. spirata*, eggs are held by the female inside her mantle cavity until the planktonic larvae hatch (Probst & Crawford, 2008: 195; Bieler & Hadfield, 1990).

There is conflicting evidence of the existence of nurse eggs in turritellines. Pilkington (1974) concluded that in *Maoricolpus roseus*, although many eggs were laid per capsule,

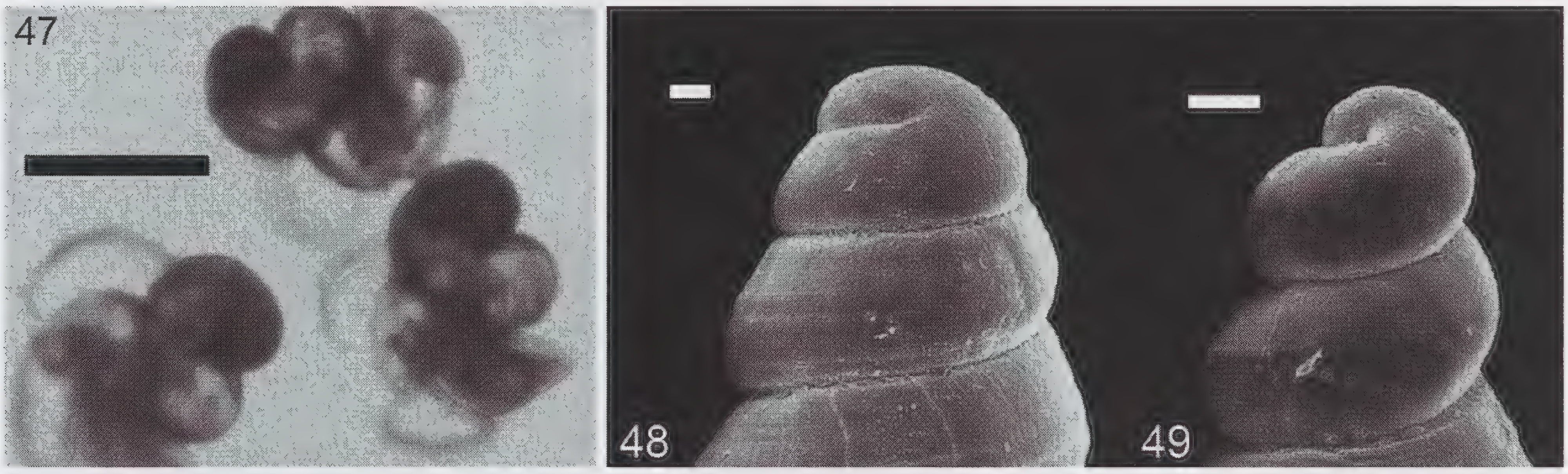








FIGS. 43–46. Turritelline eggs. FIG. 43: Individual of *T. gonostoma* with eggs, northern Gulf of California. Shell length approximately 120 mm; FIG. 44: Diagram of egg capsules of *T. communis* attached to substrate (after Fretter and Graham, 1962). Scale bar = 2 mm; FIG. 45: *Maoricolpus roseus* w/eggs (from Bax et al., 2003; photograph by Felicity McEnnulty, CSIRO Marine and Atmospheric Research, Australia; reproduced with permission); FIG. 46: Egg string of *Vermicularia spirata* (from Bieler and Hadfield, 1990). Scale bar = 2 mm.



FIGS. 47–49. Larval and early adult whorls of living turritellines. FIG. 47: Light micrograph of veligers of *Turritella gonostoma* (from Allmon et al., 1992); FIG. 48: Scanning electron micrograph of the apex of an adult shell of *T. communis* from the English Channel, showing protoconch and protoconch-teleoconch boundary; FIG. 49: Scanning electron micrograph of the apex of an adult shell of *T. variegata* from Venezuela, showing protoconch and protoconch-teleoconch boundary. Specimens 48 and 49 in the collections of the Museum of Comparative Zoology, Dept. of Invertebrate Paleontology.

most embryos abort and serve as food for those that remain, and Peréz (1930) reported that leucocytes of *Turritella* are known to be phagocytic when engulfing their own unused ova. Similarly, Bax et al. (2003: 10) found that in *M. roseus* in Tasmania, "Up to 300 + very early stage embryos were observed within egg capsules in December, but only 50–100 veligers of 100–200 µm size in January, indicating number of embryos per capsule decreases as embryo size increases". In *M. roseus*, Probst & Crawford (2008: 195), however, reported "consistent observations of high numbers of veligers (up to 50) with highly synchronized development released from egg capsules", which would not be expected if nurse eggs were an important source of pre-hatching larval nutrition. *Vermicularia spirata* does not have nurse eggs (Bieler & Hadfield, 1990).

Reproduction appears to be more or less seasonal (late winter to early summer) in all living species that have been investigated. *Turritella gonostoma* in the northern Gulf of California deposits eggs in late winter and early spring (February–April) (Allmon, 1988; Allmon et al., 1992). Spawning females of *T. variegata* were collected on the Caribbean coast of Colombia in the winter (December–February) in two consecutive years (Bandel, 1976). *Turritella communis* spawns in the English Channel in the late spring (April–July) (Lebour, 1933; Wright, 1956; Fretter & Graham, 1962; Fretter & Manly, 1979; Kennedy, 1995). In *Maoricolpus roseus,* males have active sperm in the austral spring (September–October) and females have been observed to have egg capsules in spring and summer (September–February) (Pilkington, 1974; Bax et al., 2003). Carrick (1980a, b) observed oviposition by *Gazameda gunnii* in the austral summer (January), although the eggs are brooded in this species and metamorphosed juveniles are not released by the mother for another eight months (August). *Turritella cingulata* in Chile spawns in the austral spring and summer (September–March) (Romero et al., 2003).

Direct information on larval developmental pattern is available for seven living turritelline species (Table 2). Six of these have larvae that spend at least some time in the plankton, and one broods crawl-away larvae. In the species with pelagic larvae, the duration of their time in the plankton is relatively short (i.e., long-term planktotrophic – or teleplanic – larvae are not known). *Gazameda gunnii* from Australia is the only species known to have no planktonic larval period; it broods relatively large eggs within the mantle cavity for approximately 200 days, after which crawling juveniles are released (Peile, 1922; Iredale, 1924; Carrick, 1980a, b). The discovery of large numbers of tiny juvenile shells inside the shell of a conspecific adult has led to the inference of possibly similar ovoviviparity in at least six fossil turritelline species (Table 3). "Brooding" of a different sort occurs in at least one species: as described below, female *Maoricolpus roseus* hold their eggs within the mantle cavity for some time (Bax et al., 2003; Fig. 45) before the hatching of pelagic larvae.

Images and/or descriptions of veligers are available for at least five turritelline species: *Turritella gonostoma* (Allmon et al., 1992); *T. communis* (Fretter & Pilkington, 1970);

TABLE 2. Developmental patterns of larvae in living turritelline species.

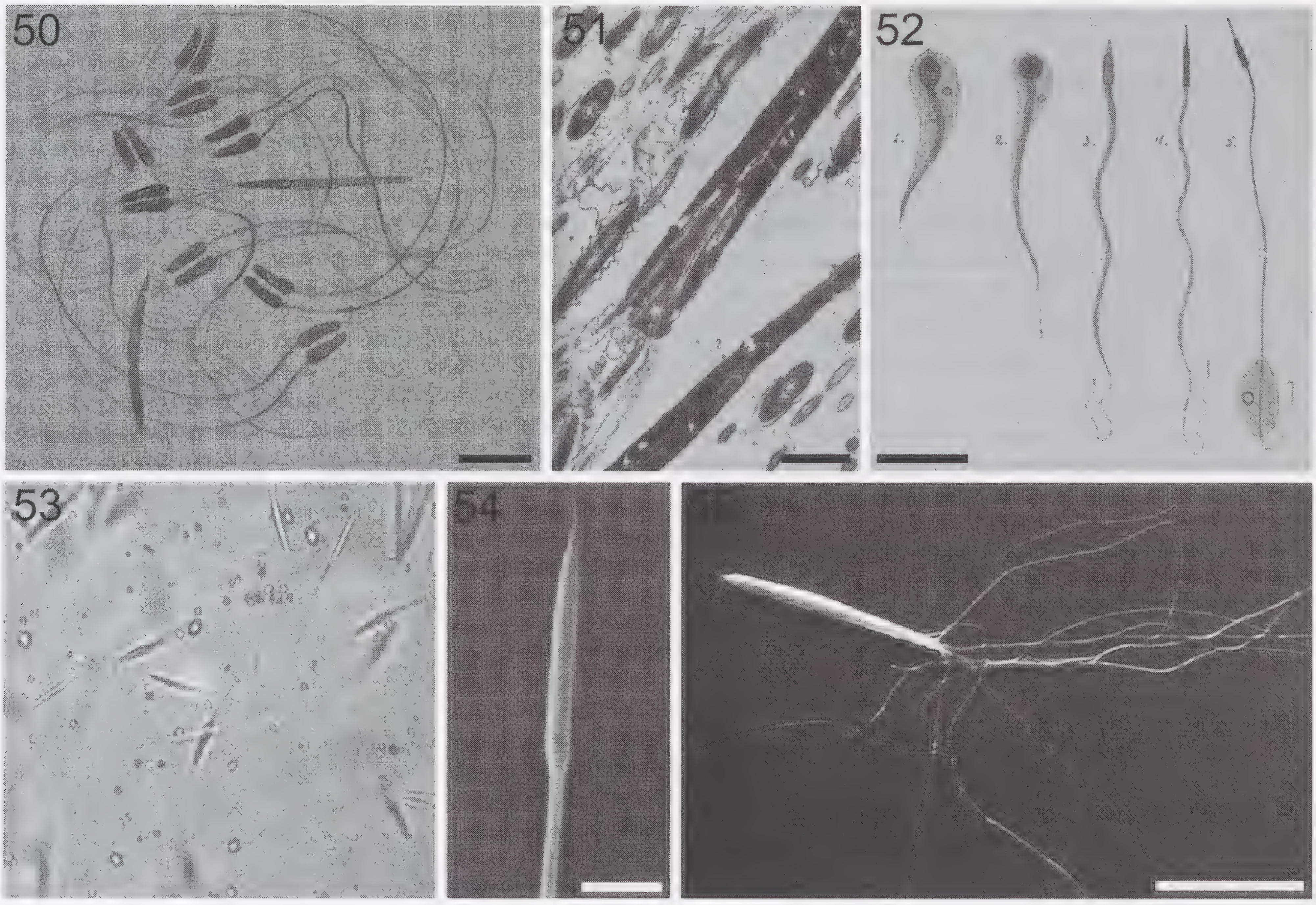
Species	Location	Planktonic phase duration (days)	Egg diameter	Reference
Turritella communis	NE Atlantic	14–21	100–139 μm	Lebour (1933); Kennedy & Keegan (1992)
Maoricolpus roseus	NZ, Australia	> 14	150 μm	Bax et al. (2003); Gunasekera et al. (2005); Probst & Crawford (2008)
Gazameda gunii	Australia	0	960–1000 μm	Carrick (1980a, b)
Turritella variegata	Venezuela	0–3	113 μm	Bandel (1976); Romero et al. (2003: 57)
Turritella gonostoma	Gulf of California	7–10	?	Allmon (1988); Allmon et al. (1992)
Turritella cingulata	Chile	?	92 μm	Romero et al. (2002, 2003)
Vermicularia spirata	Florida	?	300 μm	Bieler & Hadfield (1990)

Maoricolpus roseus (Bax et al., 2003; Gunasekera et al., 2005; Probst & Crawford, 2008); *T. cingulata* (Romero et al., 2003); and *Vermicularia spirata* (Bieler & Hadfield, 1990) (Fig. 47). Veligers of *M. roseus* have been maintained in laboratory aquaria for up to two weeks, where they were observed to feed on supplied microalgae (i.e., *Isochrysis*, *Pavlova*, *Nannochloropsis*, and *Caetoceros*) (Probst & Crawford, 2008: 193), and so should properly be termed "planktotrophic" (*sensu* Jablonski & Lutz, 1983). Apparently no direct observations of larval settlement and metamorphosis have been published.

Turritelline protoconchs consist of 2–5 smooth, rounded whorls, with the beginning of the teleoconch marked by gradual-to-abrupt appearance of one or more spiral ribs. The form of these protoconchs is generally consistent with Thorson's (1950) "apex theory" in reflecting developmental mode (Figs. 48, 49): planktotrophic species have relatively narrow, multispiral protoconchs, with the protoconch I (PI) usually clearly distinguishable from the larger protoconch II (P2); nonplanktotrophic species have larger, more rounded, paucispiral protoconchs, and the demarcation between PI and P2 is often faint or absent (Allmon, 1988; Bieler & Hadfield, 1990; see

TABLE 3. Instances of ovoviviparity in fossil turritellines reported in the literature.

Species	Age	Locality	Formation	No. of embryonic shells	Reference
Turritella alticostata	Miocene-Pliocene?	Rice's Pit, Hampton, Virginia	?	41	Antill (1974)
T. alumensis	Miocene	Alum Bluff, Florida	Choctawhatchee	48	Sutton (1935)
T. cumberlandia	Miocene	Plum Point, Maryland	Calvert	> 200	Burns (1899)
T. indenta	Miocene	Plum Point, Maryland	Calvert	"by the hundreds"	Burns (1899)
T. pilsbryi	Pliocene	Yorktown, Virignia	Yorktown	104	Palmer (1958)
T. pilsbryi	Pliocene	Yorktown, Virginia	Yorktown	47	Gardner (1948)
Zeacolpus taranakiensis	Pliocene?	Wellington, New Zealand	?	40-100	Marwick (1971a, b)



FIGS. 50–55. Sperm of three living turritelline species. FIG. 50: Cluster of paired adult euspermatozoa of *Turritella communis.* Scale bar ≈ 10 µm (from Bataillon, 1921); FIG. 51: Longitudinal section of the basal tract of a paraspermatic cell of *T. communis* (arrow indicates the insertion area of flagella; t = typical spermatozoa; g= granules). Scale bar ≈ 100 µm (from Melone et al., 1980); FIG. 52: Successive stages in the maturation of euspermatozoa of *T. communis.* Scale bar ≈ 400 µm (after Schitz, 1920); FIG. 53: Light micrograph of sperm of *Maoricolpus roseus* (from Bax et al., 2003); FIGS. 54, 55: Sperm of *Vermicularia spirata* (from Bieler and Hadfield, 1990). FIG. 54: Head of euspermatozoan. Scale bar = 2 µm; FIG. 55: Multiflagellate paraspermatozoan. Scale bar = 10 µm.

Jablonski & Lutz, 1983, for further discussion). Using this relationship, the developmental mode of a number of fossil turritelline species has been inferred (Jablonski, 1979; Dockery, 1993; Allmon, 1996; Bandel, 2006). Although some of these species have protoconchs indicative of long-term planktonic (planktotrophic) phases, most have protoconchs suggesting relatively short planktonic phases and so of relatively low dispersal potential (Allmon, 1996).

Spermatozoa

The sperm of most marine caenogastropods are of the "modified" type characteristic of species with internal fertilization (Franzén, 1955): each spermatozoan generally consists of three regions: an elongate pointed head, a long cylindrical middle piece, and a tail or flagellum (Franzén, 1955; Voltzow, 1994). Knowledge of turritelline sperm (Figs. 41, 42, 50–55) is based on data from five species: *Turritella communis* (Retzius, 1910; Bataillon, 1921; Franzén, 1955; Idelman, 1960; Melone et al., 1980; Afzelius & Dallai, 1983; Kennedy, 1995; Ishijima et al., 1999); *T. triplicata* (Schitz, 1920); *Maoricolpus roseus* (Bax et al., 2003); *T. cingulata* (Koike, 1985); and *Vermicularia spirata* (Bieler & Hadfield, 1990).

As in many caenogastropods, and especially cerithioideans (Healy & Jamieson, 1981; Healy, 1983, 1986), turritelline sperm are dimorphic: two distinct types of sperm are produced simultaneously within the male gonad of these two species. "Typical spermatozoa" (= "euspermatozoa") are capable of fertilization, and are also referred to as "eupyrene", meaning that they have nuclei containing the haploid number of chromosomes. "Atypical spermatozoa" (= "paraspermatozoa") are sterile, and can be "oligopyrene" (with only part of the haploid set) or "apyrene" (lacking nuclei altogether) (Fretter

& Graham, 1962: 338; Afzelius & Dallai, 1983; Kennedy, 1995; Ishijima et al., 1999; Pitnick et al., 2009) (Figs. 41, 42, 50–55).

The evolutionary significance of such sperm dimorphism (in gastropods as well as other groups) remains unclear, although numerous hypotheses have been proposed (Hodgson, 1997; Buckland-Nicks, 1998; Swallow & Wilkinson, 2002; Pitnick et al., 2009). The two most frequently mentioned are that paraspermatozoa serve as trophic resources (aka "provisioning" or "nurse cells") for euspermatozoa, and that they assist in transporting euspermatozoa to the ova for fertilization. Apparently neither of these hypotheses has been evaluated for cerithiacean gastropods.

In *Turritella communis*, the euspermatozoan (Fig. 42) is morphologically similar to those of other cerithioidean taxa (Franzén, 1955; Healy, 1983). The acrosome is elongated and conical, has a deep posterior invagination, and generally measures approximately 1.5 µm along its long axis; the even more elongated middle piece measures around 60 µm in length, and the free portion of the tail 40 µm (Afzelius & Dallai, 1983). The euspermatozoa of *T. communis* are often paired (Bataillon 1921; Franzen, 1955; Afzelius & Dallai, 1983) (Figs. 42, 50), as are those of *Vermicularia spirata* (Bieler & Hadfield, 1990) (Fig. 54), and can swim backward as well as forward (Afzelius & Dallai, 1983; Ishijima et al., 1999). Pairing of spermatozoa has also been described for three other animal groups (American marsupials, thrips, and dytiscid water beetles). The functional and adaptive significance of pairing are unclear, but have been assumed to enhance swimming ability and so ability to reach and penetrate the egg (Sivinski, 1979; Afzelius & Dallai, 1983), although the paired sperm do not swim faster than single sperm (Ishijima et al., 1999), in contrast to the situation in other animal groups (Pitnick et al., 2009: 104). In turritellines, the pairing occurs at the acrosome and nucleus, with the middle pieces and tail free and mobile (Idelman, 1960; Afzelius & Dallai, 1983).

The paraspermatozoan in *Turritella communis* (Melone et al., 1980; Figs. 50, 52) is also similar to those in other cerithioid species (Healy, 1986). It is composed of two parts: an elongate subconical "head" approximately 20 µm long and 1.5 µm in diameter, and a set of 8–9 flagella. The parasperatozoa of *Vermicularia spirata* are multiflagellate (Bieler & Hadfield, 1990; Fig. 54).

GROWTH

In at least two species (*Turritella communis* and *Maoricolpus roseus*), shell length is highly correlated to body mass (Thorson, 1965; Taylor, 1998; Fig. 56). If this pattern holds in the rest of the group, then shell size is a valid proxy for body mass in both living and fossil species, which would allow estimation of biomass from shell size alone.

Age of reproduction in living turritellines has not been determined by direct observation. Wright (1956) observed well-developed gonads in individuals of *Turritella communis* as small as 23 mm in length. According to the growth curves calculated by Cadée (1968), this corresponds to an age of less than one year. The life span of *T. communis* is unknown. Maximum reported size is approximately 45 mm; this corresponds to an age of just over two years on Cadée's curve. In contrast, J. B. Buchanan (pers. comm., 1987) attempted to age individuals of *T. communis* by counting collabral growth lines, and on this basis, suggested longevity of at least 15 years for this species, with population modes of 10–11 years. According to Carrick (1980a), reproduction in *Gazameda gunnii* begins when the adults are 2.5–3 years of age, and is repeated annually throughout a lifespan of 6–7 years.

Oxygen isotope sclerochronology (Jones, 1998) has been used to estimate age and growth rate for more than a dozen fossil and living turritelline species (Fig. 57). These data suggest that most species live to be no more than 3–5 years old and that growth is more rapid in juvenile stages. Two different studies of age and growth rates via isotopic analysis in living *Maoricolpus roseus* (Allmon et al., 1994; Scott, 1997) suggest that age and size of maturity in this species may vary between locations (Bax et al., 2003: 10). Scott (1997) found that shell growth was seasonal, with the most rapid growth during the warmest months, particularly during the first year of life, and that growth ceases at temperatures below 13°C and above 17°C.

Several authors have made circumstantial arguments for a positive correlation between abundance of potential food (phytoplankton) and turritelline shell size (Allmon et al., 1994; Teusch et al., 2002; Pietsch et al., 2007; Probst & Crawford, 2008), but this relationship has not been tested experimentally.

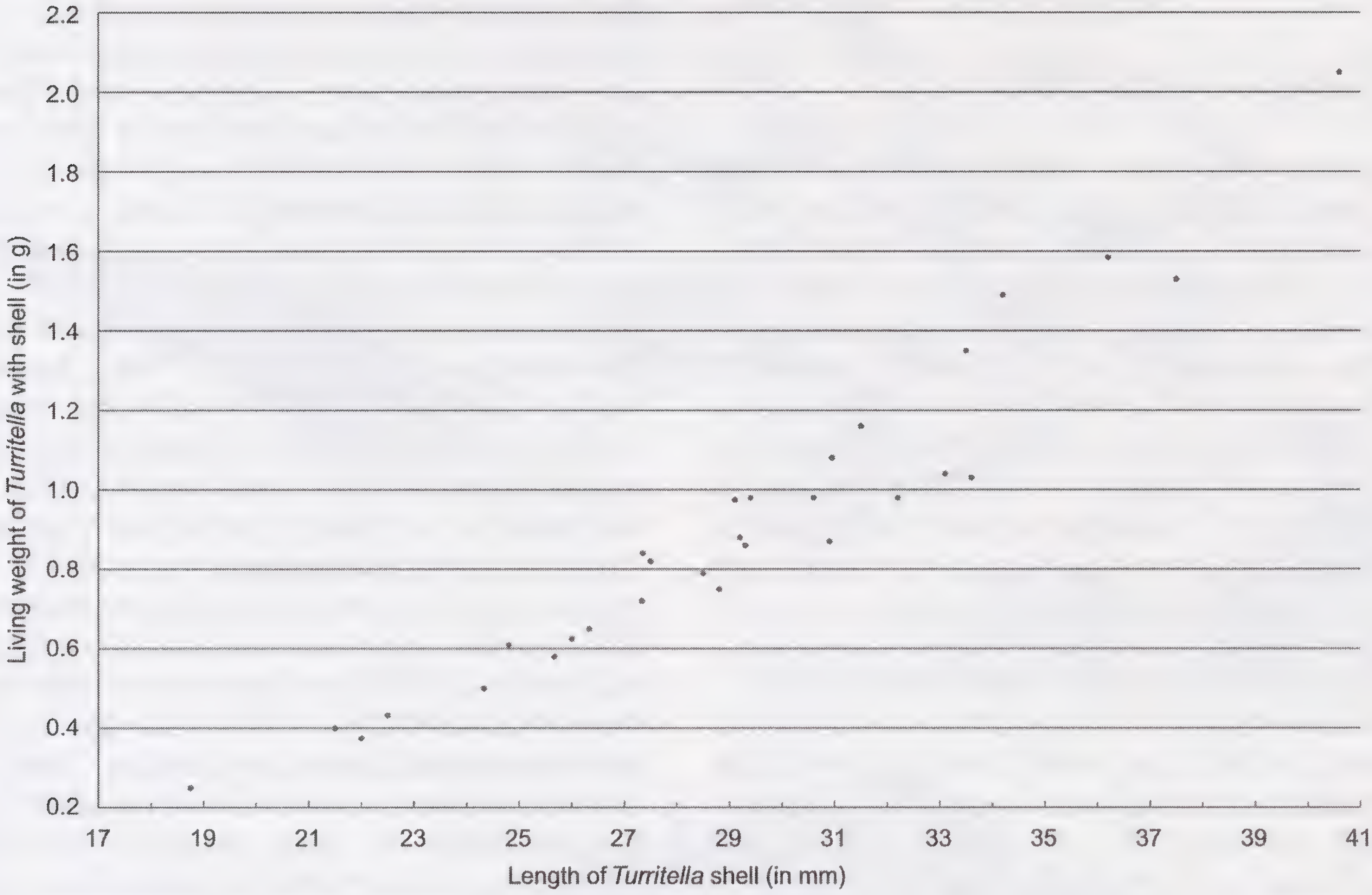


FIG. 56. Length to body weight of *T. communis* (from Thorson, 1965).

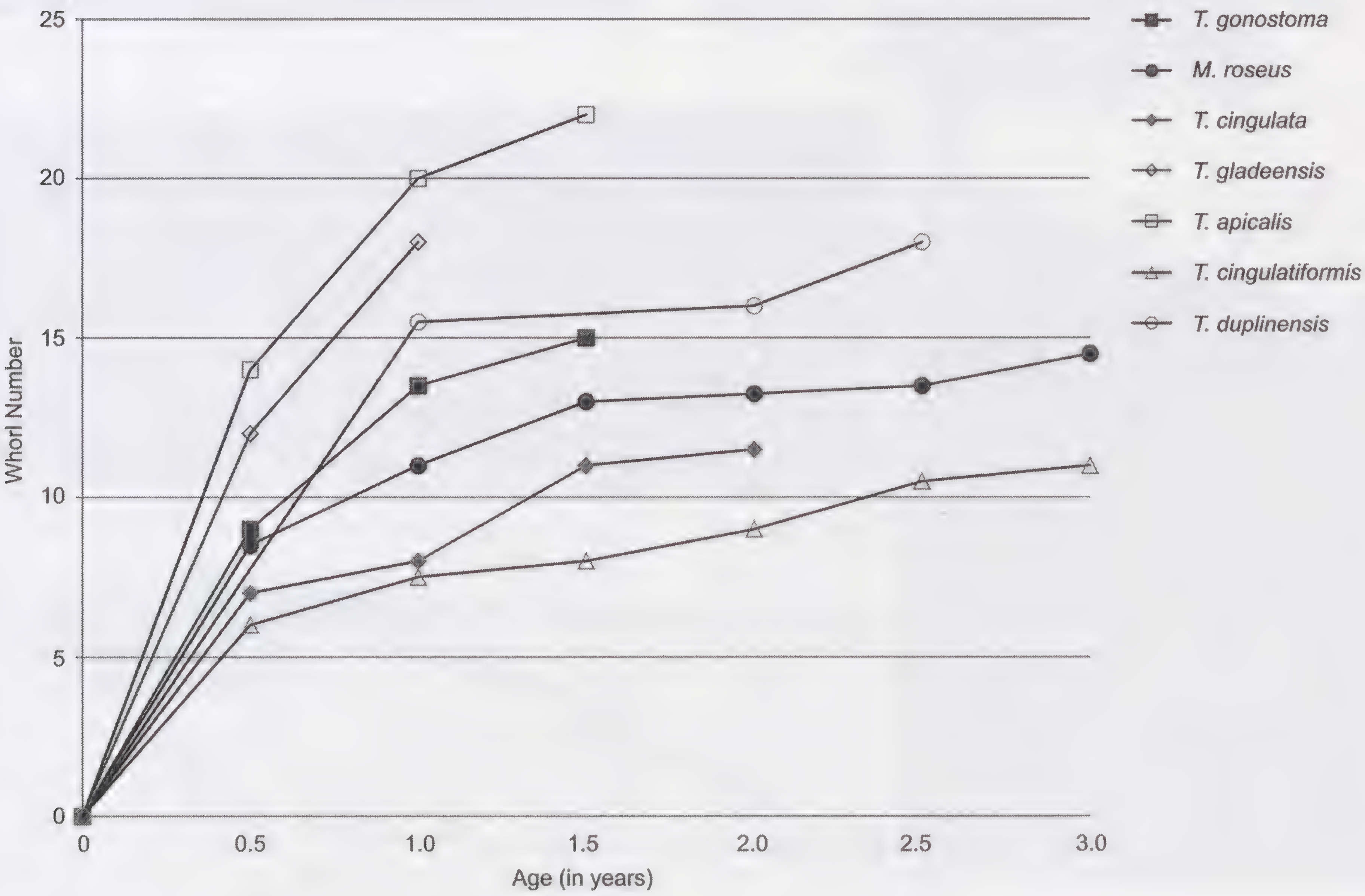


FIG. 57. Growth curves of fossil and Recent turritelline species, based on oxygen isotope sclerochronology. Data on *T. duplinensis* courtesy of Elizabeth Petsios. All other data from Jones (1998).

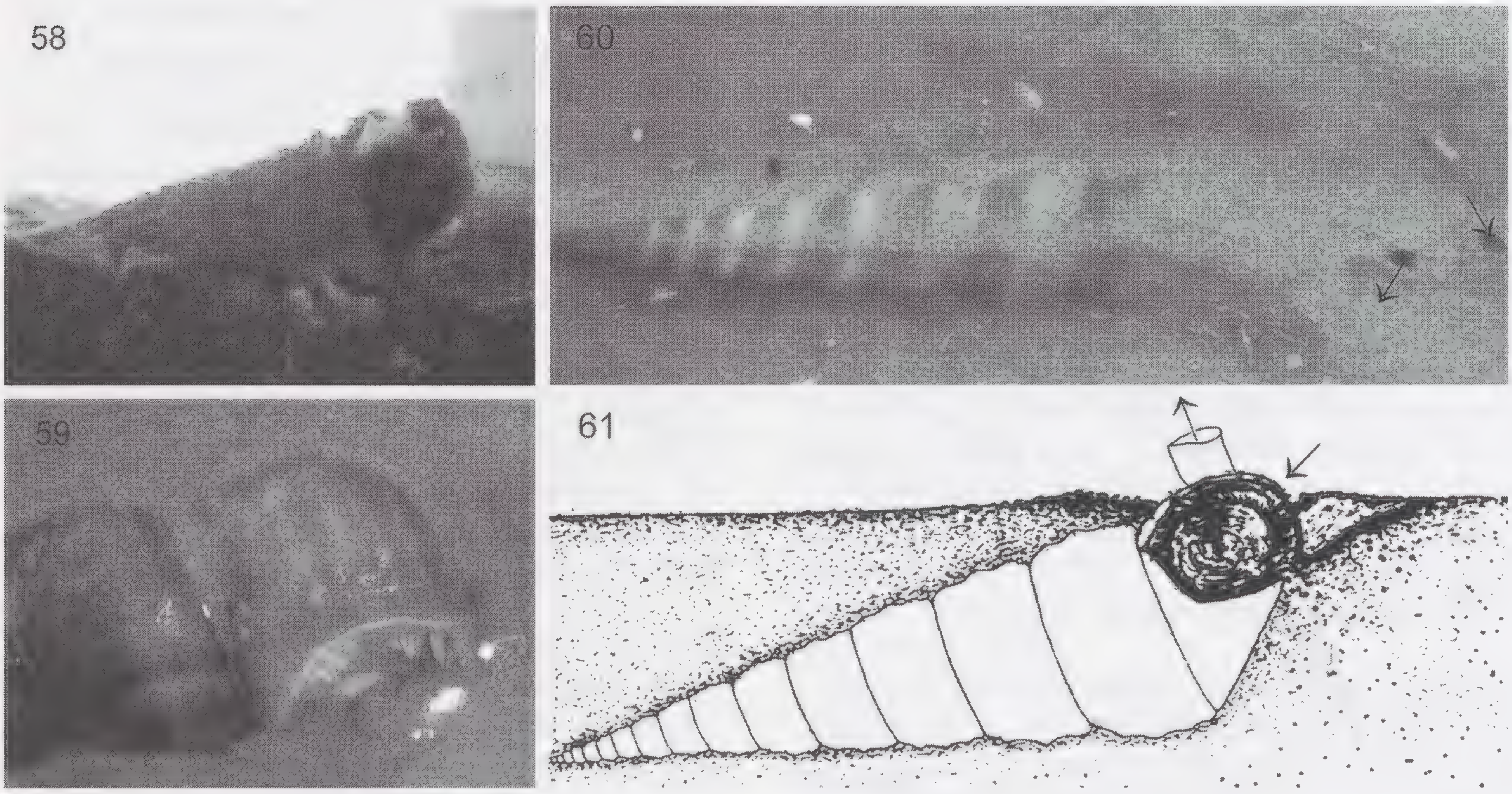
ECOLOGY

Life Position and Behavior

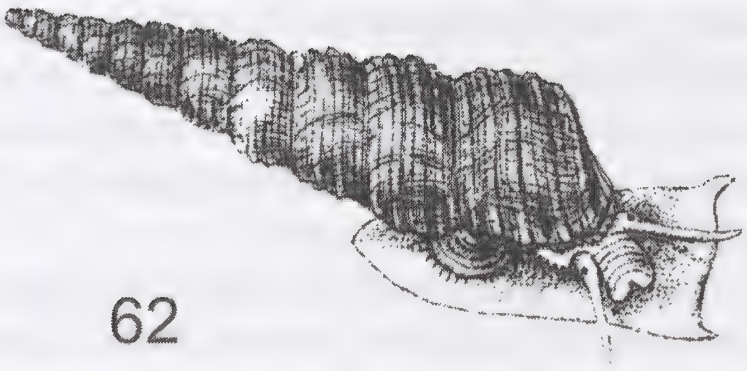
Healthy free-living adult turritellines most frequently assume two orientations on their usual substrata of soft mud or sand (Figs. 58–61). The first, assumed when at rest and suspension feeding, is with the long axis of the shell sub-parallel to the sediment surface and the aperture perpendicular to the substratum. The other, again with the long axis parallel to the sediment, but with the aperture facing the substratum, is assumed when the animal is crawling or burrowing. At least some species may regularly assume other orientations, for example when inhabiting more uneven (e.g., rocky) substrata (Allmon et al., 1994).

Some published illustrations have depicted turritellines with the animal crawling along the substratum with the shell elevated at approximately 45° (Figs. 62, 63), but this has apparently never been verified by reliable first-hand observation. The notion may have originated with Reeve (1860: 131), who wrote that: "The Turritellae [sic] are apparently a strong muscular group of mollusks, the disk being surmounted by a stout pedicle, by the strength of which the shell is borne up at an angle, but not allowed to trail upon the ground, as in the Cerithia [sic] and other elongated forms." The source of Reeve's comments is unclear, especially given that Kiener (1834) had already published a much more realistic illustration of a living turritelline, showing the shell being dragged along the substratum (Fig. 64).

Turritellines have long been thought to be essentially sedentary (Yonge, 1946; Marwick, 1957a; Bandel, 1976), and all living species for which observations have been recorded do indeed spend much of their time more or less stationary in their feeding orientation, either on top of or buried shallowly in the sediment. Because of this, they have a reputation of not being able to crawl long distances. Yet this inference may be unjustified, and movement may play a more important role in their ecology than has been recognized previously (Allmon, 1988). For example, patterns of seasonal appearance and disappearance of some species in particular areas, or of the absence of juveniles in many mass accumulations, may be due to movement over some distance (Wright, 1956; Allmon, 1988; Allmon et al., 1992; Chilcott, 1996, cited in Bax et al., 2003). Kennedy (1995) also demonstrated that *T. communis* "has a far greater



FIGS. 58–61. Normal feeding life orientation of living turritellines. FIG. 58: *Turritella banksi* from Panama, taken in aquarium; FIGS. 59, 60: *T. duplicata* from Thailand, taken in the field (courtesy of R. Waite). FIG. 59: View of body whorl of an individual buried in sediment, showing palial tentacles at edge of mantle cavity; FIG. 60: View of an entire buried individual, with arrows indicating direction of water flow into inhalant and out of exhalent openings; FIG. 61: Diagram showing pattern of water flow of an individual in this orientation, shallowly buried in sediment (modified from Healy & Wells, 1998).



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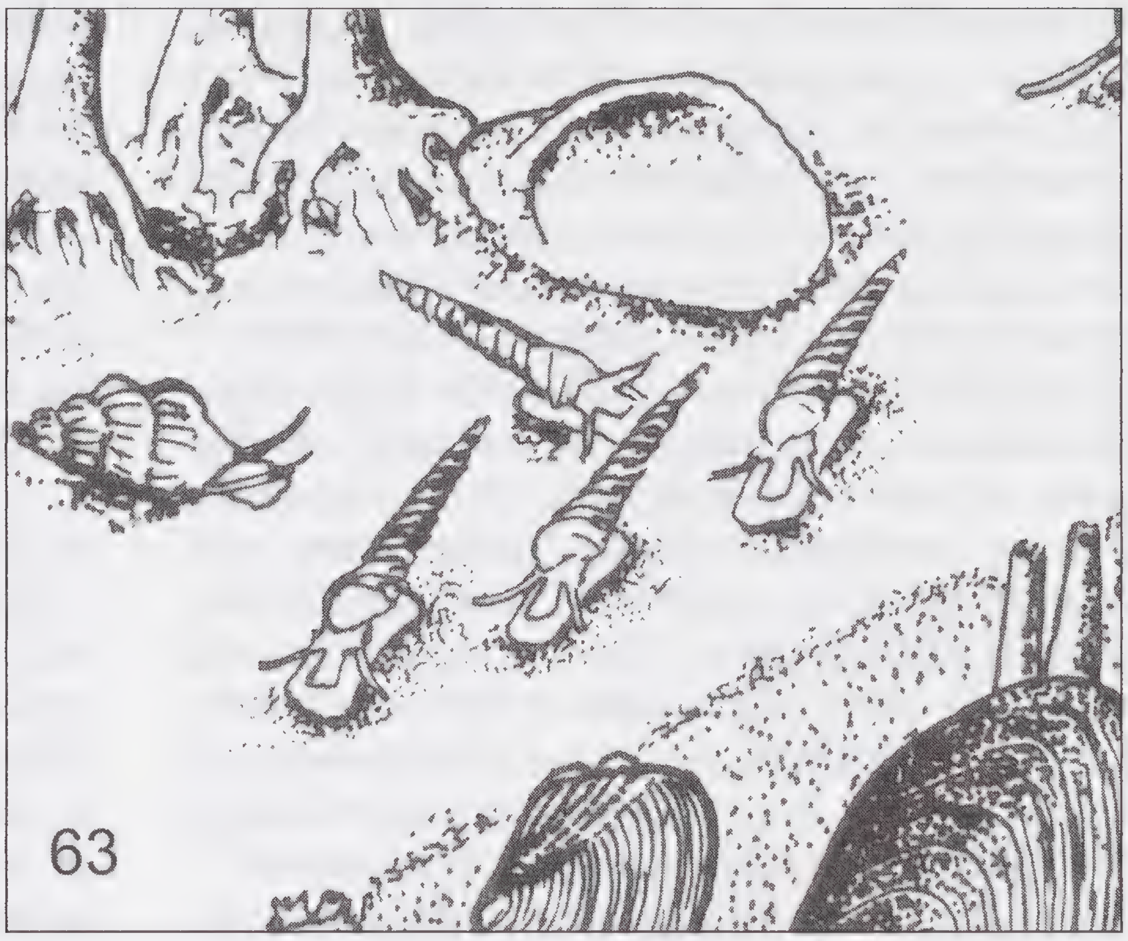

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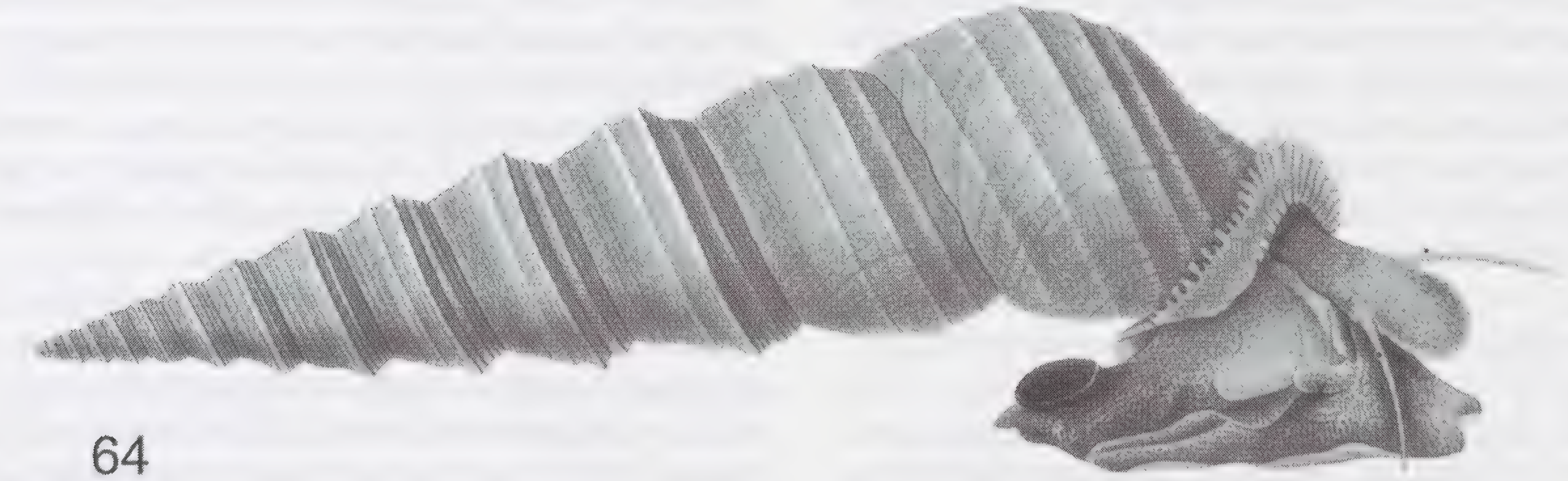

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FIGS. 62–64. Previous reconstructions of orientation of living turritellines while crawling on substrate surface. Figs. 62 and 63 are incorrect reconstructions showing the shell carried at an angle above the substrate, Fig. 64 is correct, showing the shell dragging on the substrate; FIG. 62 from Adams and Adams (1858), FIG. 63 from McKerrow (1978), FIG. 64 from Kiener (1843).

capacity for movement than was believed". Active crawling across the surface of soft substrata, leaving recognizable traces, has been documented in several living turritelline species (Allmon, 1988; Allmon et al., 1992; Kennedy, 1995; De, 1997, 2000; Allmon, unpublished observations; R. Waite, pers. comm.).

Burrowing behavior in turritellines has also been documented in a number of species (e.g., *Turritella communis* around the British Isles [Yonge, 1946; Kennedy, 1995]; *T. terebra* in Hong Kong [Hickman, 1983]; *T. variegata* in the southern Caribbean [Bandel, 1976; Petuch, 1976]; *T. gonostoma* in the Gulf of California [Allmon, 1988; Allmon et al., 1992]; *T. tricarinata* in the Mediterranean [Sartenaer, 1959]; *T. trisulcata* in the Red Sea [Allmon, 1988]; *T. banksi* in Panama [Allmon, unpublished observations]; *T. duplicata* in Thailand [R. Waite, pers. comm.]; and *M. roseus* in New Zealand and Australia [Allmon et al. 1994]. In all of these species, both crawling and burrowing is accomplished by first extending the foot over or into the sediment, and then pulling the rest of the body and shell forward in a series of abrupt but seemingly laborious heaves or jerks.

Although *Vermicularia*, with its uncoiled shell, is clearly modified for an almost completely sessile adult mode of life, even it can and does move (Gould, 1969; Hughes, 1985), extending its propodium forwards to grip the substratum, and then pulling the animal forward. Individuals have even been known to detach themselves from the substratum "by radular abrasion of the cement" (Hughes, 1985: 323). It is not clear when or why this occurs.

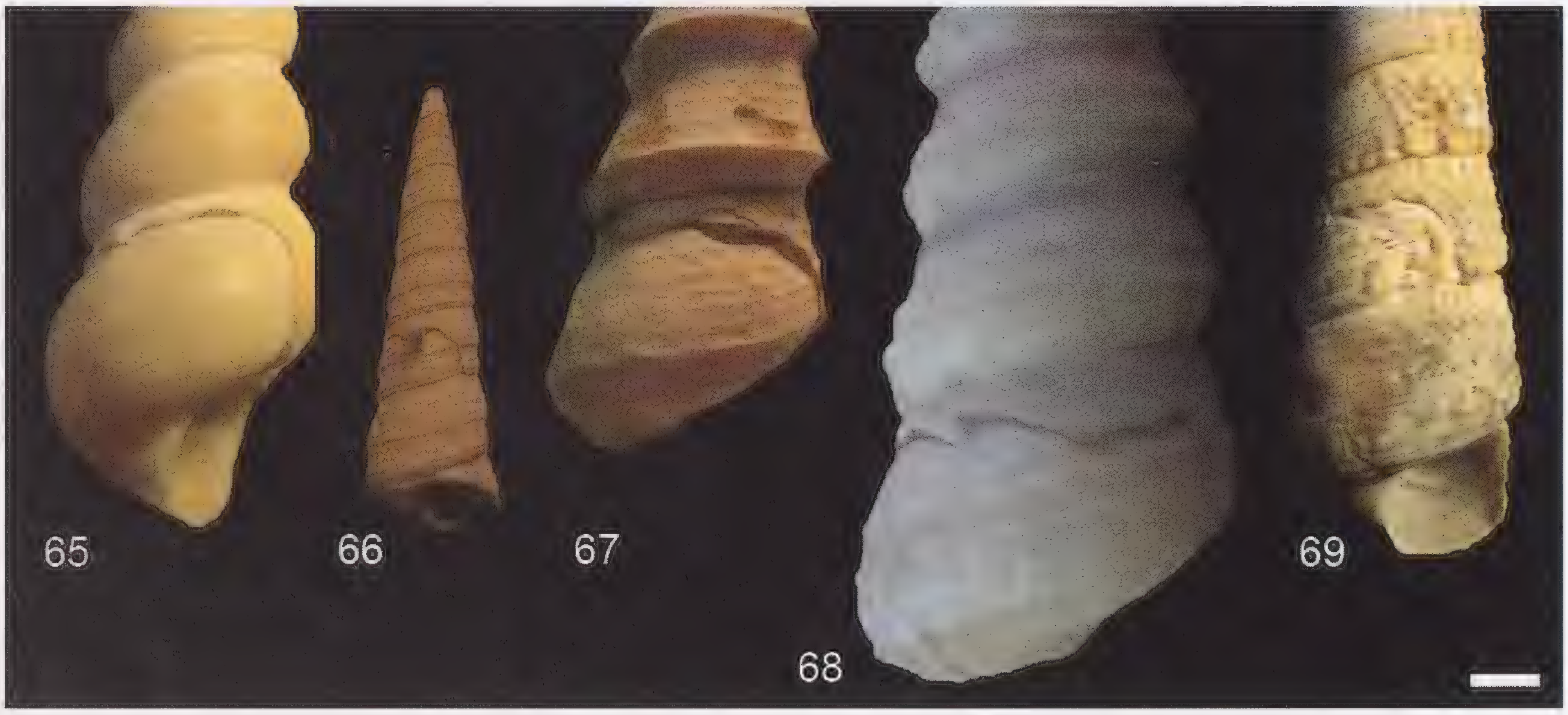
Bieler (2004) reported observing specimens of *Vermicularia* in the western Atlantic attached to a wide variety of substrata (e.g., sponges, hard coral, empty shells, rocks, algae, etc.). The occurrence of coiling in these instances, he suggested, may be the result of a balance between secure attachment and maintaining the aperture in a suitable position to feed from local currents (Bieler, 2004, and pers. comm., March 2011).

Several turritelline species have been observed in an almost vertical orientation, with the apex buried in the sediment and the aperture several centimeters above the sediment surface (Pinn, 1990; Allmon et al., 1992, 1994). Pinn (1990) reported "hundreds" of *Turritella duplicata* and *T. attenuata* in this orientation. He stated that "about half the shells stand upright at an angle of 90 degrees and the other half slanting at approximately 45 degrees". Pinn suggested that the snails do not attain this orientation by moving backward into the sediment, but by first digging down and then upward, after which they are exposed by tides or currents. Such behavior, however, has never been directly observed, and other observations suggest that such a posture may result from accidental orientation by currents (Allmon et al., 1994; R. Waite, pers. comm.).

Feeding

Although several early authors concluded that *Turritella communis* is a non-selective deposit feeder (Petersen, 1913; Hunt, 1925; Merriam, 1941), later studies showed that it is predominantly a ciliary suspension feeder (Graham, 1938; Yonge, 1946). As described above, food particles enter the mantle cavity where they are captured by the gill, and then transferred to the mouth via a mucus strand. Allmon et al. (1992) observed *T. gonostoma* in the laboratory and found that its feeding rates were much lower than expected compared to both other suspension feeding gastropods (e.g., *Crepidula*) and bivalves.

Yonge used observations of suspension feeding in *Turritella communis*, together with the generally reduced odontophore, radula, and salivary glands in this species, to generalize about the entire group, stating that "*Turritella* is an exclusively ciliary feeder" (1946: 379), and this was the prevailing view for the next half-century. Fretter (1975), however, pointed out that neither Graham nor Yonge made any observations on animals deprived of their normal food, when they might behave differently. A detailed study of the feeding behavior of the Australian turritelline *Gazameda gunnii* by Carrick (1980a) found that this species is not only a ciliary suspension feeder in the style of *T. communis,* but also a deposit feeder. *G. gunnii* apparently traps sediment with mucus strings extruded from the mantle cavity, and consumes these strings by means of its radula, much in the way that *T. communis* does the mucus that carries food particles out of its mantle cavity.



FIGS. 65–69. Breakage-and-repair scars in fossil and modern turritelline shells. FIG. 65: *Turritella cerea*, Recent, Darwin, Northern Territory, Australia, PRI Collection; FIG. 66: *Turritella* sp., Late Miocene, Darien, Panama, Natural History Museum Basel (NHMB) Collection; FIG. 67: *T. robusta*, Late Miocene, Darien, Panama, NHMB Collection; FIG. 68: *T. duplicata*, Recent, Penang, Malaysia, PRI Collection; FIG. 69: *T. variegata*, Recent, Venezuela, PRI Collection. Scale bar = 5 mm.

Analyses of gut and fecal contents show that *G. gunnii* consumes a range of material including diatoms, sponge spicules, bryozoan and crustacean skeletal fragments, and coarse siliceous sediment grains. *Gazameda gunnii* furthermore appears to partition its mode of feeding seasonally, according to local phytoplankton abundance, feeding on sediment when it is low, but acting as a ciliary suspension-feeder when it is high (Carrick 1980a).

In *Vermicularia*, feeding occurs in a similar way (Hughes, 1985; Figs. 7–11). The operculum protrudes from the shell and the head is approximately flush with the aperture. The sole of the metapodium faces upward, and the propodium is extended vertically with its sole facing forward. Pallial tentacles divide the entrance to the mantle cavity into a left incurrent and a right excurrent aperture. As in other species described above, particles in the incurrent stream are moved along the ctenidial filaments to the floor of the mantle cavity where they become bound in mucus, to a food groove to the right of the head, from the tip of which they are picked up by the radula and ingested.

Predators

Living turritellines are eaten by a wide variety of invertebrate and vertebrate predators (Table 4), including fish, turtles, seastars, crabs, and other gastropods. With few exceptions (Gaymer & Himmelman, 2008), however, living turritellines are occasional prey, and seem not to be especially heavily preyed upon by, or to be the principal prey of, any living predator.

Fish and turtles appear to consume turritellines by swallowing them whole or breaking them in their jaws and swallowing pieces (this is not always specified in the literature; Redon et al., 1994; Spring & Gwyther, 1999). Seastars evert their stomachs and envelope the apertural end of the shell, removing the soft parts and leaving little if any mark on the shell (Allmon et al., 1994). The exact means by which decapod crustaceans consume turritellines is not explicitly described in the literature, but at least some species swallow enough of the shell for it to be identifiable (Goñi et al., 2001; Fanelli & Cartes, 2004; Léon & Stotz, 2004).

Most fossil and recent turritelline shells show traces of breakage and repair (Figs. 65–69). Although some of this breakage is undoubtedly due to abiotic factors, resulting for example, from rolling of the shell by waves, many repaired breaks extend far behind the aperture, forming a deep repair scar of the type generally attributed to unsuccessful predation by decapod crustaceans that peel the shell back from the shell opening (Vermeij, 1982, 1983). Despite the widespread occurrence of such repair scars, however, there appear to be no published accounts of living decapods preying on turritellines by such peeling. As mentioned above, at least some turritelline species can retract into their shell more than 200° behind the unbroken aperture, the flexible and fringed operculum bending to allow withdrawal and simultaneous maintenance of water flow around it (Ankel, 1971; Fretter & Graham, 1981; Kilburn & Rippey, 1982: 52; pers. obs.); this is seemingly a useful defense against peeling predators.

There similarly appear to be no published accounts of direct observation of drilling predation on living turritellines, yet both fossil and recent turritelline shells frequently bear holes indicative of successful drilling predation (Dudley & Vermeij, 1978; Allmon et al., 1990). As is true for many other prey taxa, the identity of drilling predators on turritellines can be determined at least to some degree by the shape of the drillhole: naticid snails (family Naticidae) usually drill a beveled or parabolic hole, whereas muricid snails (family Muricidae) and octopus drill holes with relatively straight sides (Kitchell et al., 1981). Using this technique, a number of studies indicate that naticids are the most frequent drilling predators on fossil and living turritellines (Allmon et al., 1990; Tull & Böhning-Gaese, 1993; Hagadorn & Boyajian, 1997).

Other predatory gastropods attack turritellines through the aperture. In northern Venezuela, for example, *T. variegata* is preyed upon by at least five gastropod species, all of which apparently feed through the aperture of the snail (Petuch, 1976) (Table 4).

Parasites

At least four living turritelline species have been observed to be infected by trematode parasites (Platyhelminthes: Digenea) (Table 5), although these relationships have been studied in greatest detail in *Turritella communis* from the northeastern Atlantic. Trematodes are the most common metazoan parasites of gastropods (Poulin & Mouritsen, 2003). Like most trematodes, those infecting *T. communis* have a complex life cycle with three hosts (Kearn, 1998; Cribb et al., 2000): the first is the snail, the second a fish (usually a clupeoid or gadoid; Rothschild & Sproston, 1941; Wright, 1956; MacKenzie, 1985), and the third (the

TABLE 4. Predators of living turritelline species reported in the literature. References: 1 = Bax et al. (2003); 2 = Jones & Slinn (1956); Schafer (1972); 3 = Hunt (1925); Christensen (1970); 4 = Allmon et al. (1994); 5 = Petuch (1976); 6 = DuShane & Brennan (1969); 7 = K. Gowlett-Holmes (pers. comm.); 8 = Thorson (1965); 9 = Edgar (2000); 10 = Morton (1994); 11 = Spring & Gwyther (1999); 12 = Oliva & Carvajal (1984); 13 = León & Stotz (2004); 14 = Goñi et al. (2001); 15 = Redon et al. (1994); 16 = Ouannes-Ghorbel & Bouain (2006); 17 = Casale et al. (2008); 18 = Ortiz (2008); 19 = Davide et al. (2005); 20 = Fanelli & Cartes (2004); 21 = Gaymer & Himmelman (2008); 22 = Márquez (1990); 23 = Fehri-Bedoui et al. (2009); 24 = Matthews (1968); 25 = Paulay (2000); 26 = Albert (1995); 27 = Politou & Papaconstantinou (1994); 28 = Carpentieri et al. (2010); 29 = Nagabhushanam (1964); 30 = Fuentes (1981); 31 = Dodd (2009); 32 = King & Clark (1984); 33 = D. H. Graham (1939); 34 = Conway & Guinea (2011).

	Predator	Prey species	Location	Reference
Fish				
Elasmobranchii	Heterodontidae (horn sharks)			
	Heterodontus portusjacksoni	*M. roseus*	SE Australia	1
	Parascylliidae (collared carpet sharks)			
	Parascyllium ferrugineum	*M. roseus*	SE Australia	1
	Scyliorhinidae (cat sharks)			
	Asymbolus sp.	*M. roseus*	SE Australia	1
	Triakidae (hound sharks)			
	Mustelicus lenticulatus	*M. roseus*	New Zealand	4, 32
	Myliobatidae (eagle rays)			
	Myliobatis australis	*M. roseus*	SE Australia	1
	Urolophidae (round stingrays)			
	Urolophus cruciatus	*M. roseus*	SE Australia	1
Albuliformes	Albulidae (bonefishes)			
	Albula glossodonta	*T. cingulifer*	Tarawa	25
Batrachoidiformes	Batrachoididae (toadfish)			
	Amphichthys cryptocentrus	*T. exoleta*	Brazil	24
Scorpaeniformes	Triglidae (searobins)			
	Chelidonichthyes kumu	*M. roseus*	SE Australia	1
Perciformes	Citharidae (flounders)			
	Citharus lingulatus	*T. communis*	Mediterranean (Spain, Italy)	15, 27, 28
	Labridae (wrasses)			
	Notolabrus tetricus	*M. roseus*	SE Australia	1
	Pseudolabrus psittaculus	*M. roseus*	SE Australia	1
	Ophthalmolepis lineolatus	*M. roseus*	SE Australia	1
	Symphodus (Crenilabrus) tinca	*T.* sp. (probably *T. communis*)	Mediterranean (Tunisia)	16
	Semicossyphus maculatus	*T. cingulata*	Chile	30
	Gadidae (cods)			
	Gadus morhua	*T. communis*	North Sea (Kattegat)	2
	Gadus merlangus	*T. communis*	Irish Sea	29
	Melanogrammus aeglefinus	*T. communis*	Norway	26
	Trisopterus minimus	*T. communis*	Greece	27
	Moridae (morid cods)			
	Pseudophycis bachus	*M. roseus*	New Zealand	33

(continues)

(continued)

	Predator	Prey species	Location	Reference
	Haemulidae (grunts)			
	Anisotremus scapularis	*T.* sp. (probably *T. cingulata*)	Chile	12
	Uranoscopidae (stargazers)			
	Kathetostoma leave	*M. roseus*	SE Australia	1
	Callionymidae (dragonets)			
	Synchiropus calauropomus	*M. roseus*	SE Australia	1
	Pinguipedidae (sandperches)			
	Pinguipes chilensis	*T. cingulata*	Chile	18
	Cheilodactylidae (morwongs)			
	Cheilodactylus variegatus	*T. cingulata*	Chile	18
	Sparidae (porgies)			
	Pagellus acarne	*T. communis*	Mediterranean (Tunisia)	23
	Pagrus auratus	*M. roseus*	New Zealand	31
Tetraodontiformes	Monacanthidae (filefishes)			
	Parika scaber	*M. roseus*	SE Australia	1
	Meuschenia freycineti	*M. roseus*	SE Australia	1
	Diodontidae (porcupine fishes)			
	Diodon nichthemerus	*M. roseus*	SE Australia	1
	Allomycterus pillatus	*M. roseus*	SE Australia	1
Turtles				
	Lepidochelys olivacea	*T. terebra*	New Guinea	11
	Lepidochelys olivacea	*T.* sp.	Mexico	22
	Caretta caretta	*T. communis*	Mediterranean	17
	Caretta caretta	*T. terebra*	N. Australia	34
Decapods				
	Cancer polyodon	*T. cingulata*	Chile	13
	Palinurus elephas	*T.* sp. (probably *T. communis*)	NW Mediterranean	14
	Plesionika edwardsii	*T.* sp. (probably *T. communis*)	SW Mediterranean	20
Asteroids				
	Astropecten sp.	*M. roseus*	SE Australia	7
	Heliaster helianthus	*T. cingulata*	Chile	18, 21
	Luidia sp.	*M. roseus*	SE Australia	7
	Meyenaster gelatinosus	*T. cingulata*	Chile	18, 21
	Patitiella regularis	*M. roseus*	Tasmania	1
	spp.	*T. communis*	English Channel	3
	spp.	*T. anactor*	Gulf of California	6
	Uniophora spp.	*M. roseus*	Tasmania	1
Echinoids				
	Paracentrotus lividus	*T. communis*	Mediterranean (Croatia)	19

(continues)

(continued)

	Predator	Prey species	Location	Reference
Gastropods				
	Xymene ambiguus	*M. roseus*	New Zealand	4
	Scaphander lignarius	*T. communis*	Denmark	8
	Fasciolaria tulipa	*T. variegata*	Venezuela	5
	Melongena melongena	*T. variegata*	Venezuela	5
	Chicoreus brevifrons	*T. variegata*	Venezuela	5
	Voluta musica	*T. variegata*	Venezuela	5
	Phyllonotus globosus	*T. variegata*	Venezuela	5
	Pleuroploca australasiae	*M. roseus*	Tasmania	1, 9
	Rapana bezoar	*T. bacillum*	Hong Kong	10

primary or "definitive" host) a bird or fish. Most trematodes infecting marine gastropods have seabirds as definitive hosts (Wright, 1971). In the case of at least one species infecting *T. communis* (*Cercaria doricha* Rothschild, 1935), however, definitive hosts have been identified as including several fish species (*Lophius piscatorius* Linnaeus, 1758; *Scophthalmus maximus* Linnaeus, 1758; *Squatina squatina* Linnaeus, 1758; *Gadus pollachius* Linnaeus, 1758; *Raja* spp., *Trigla* spp.) (Fretter & Graham, 1962: 610).

In trematodes infecting marine gastropods, the eggs are released from the primary host via feces into the water, from which they are ingested by the snail (Wright, 1971). Within the snail, the parasite passes through three stages or generations (Cribb et al., 2000). First the eggs hatch into a free-swimming stage called a miracidum (which have been found in the stomach and intestine of *T. communis* [Wright, 1956]). The miracidia encyst in the snail's body wall in structures known as sporocysts, inside which the parasite replicates asexually, producing tiny embryos, known as redia. These then mature into a motile form called the cercaria which, after a period of at least 6–7 months (Wright, 1956: 32), emerge from the snail via the mantle cavity (Wright, 1956: 39). In *T. communis*, emergence occurs mainly during a period of about four months in spring and summer (Wright, 1956; MacKenzie, 1985). On emergence, the cercariae swim for a period of about two days (Ginetsinskaya, 1970) before being ingested by the second (intermediate) host fish (MacKenzie, 1985). In the fish, the parasites settle in the intestine, in which they develop into a encysted stage called a metacercaria, and where they can remain for 10 years or more (MacKenzie, 1985). When the intermediate fish host is eaten by the primary bird or fish host, the parasite reproduces sexually and lays eggs (Wright, 1971), and the cycle starts again.

Identification of species in Digenea is often difficult. The morphological differences between different species in the adult stage may be very small, but species can have widely different types of life cycles and morphologically distinct larvae (Wright, 1971). Knowledge of all of the different stages in these life cycles is very incomplete, and the cercaria stage is usually the best known (Cribb et al., 2000). This is the case for most of the forms observed to infect *Turritella communis*, most of which have been assigned only to the "genus *Cercaria*" (Table 5). At least three of these forms ("*C. rhodometopa*", "*C. doricha*", and "*C. pythionike*") are known to be larval stages of one or more species of the genus *Renicola* (Wright, 1953, 1956; Stunkard, 1964; MacKenzie, 1985) in the family Renicolidae. Renicolid trematodes are known to be parasites in the kidneys of birds and the family includes more than 50 species (Wright, 1971; Yamaguti, 1971; Munyer & Holloway, 1990).

The effects of trematode parasites on infected marine gastropods are poorly studied. Parasites are known to be important components of shallow marine ecosystems (Rohde, 1993; Mouritsen & Poulin, 2002; Poulin & Mouritsen, 2003; Thompson et al., 2005; Larsen & Mouritsen, 2009), and trematodes can cause major fitness reductions in their snail hosts (Poulin & Mouritsen, 2003). They have therefore been cited as potentially significant influences on marine gastropod evolution (Ruiz, 1991; Krist, 2001; Poulin & Mouritsen, 2003). The outcome of trematode infection in many mollusks is disappearance of the gonad (Laukner, 1980; Mouritsen & Poulin, 2002), and may also include decreased growth and increased mortality (Laukner, 1980; Huxham et al., 1993; Lafferty, 1993). The sporocysts of at least one trematode species, *Cercaria doricha*, are known to cause the disappearance of the gonad of *Turritella communis*, apparently by starving it of nourishment, but do not otherwise appear to harm the snail (Pérez, 1936; Negus, 1968). Bieler & Hadfield (1990:207) reported that 17% of 77 specimens of *Vermicularia spirata* they examined "were castrated by heavy trematode infections of the gonads". Pelseneer (1926) reported that trematode infestation affected sex ratio in *T. communis*. Trematode infection has been shown to cause changes in shell morphology in a variety of gastropods (Krist, 2000; Hay et al., 2005; Miura et al., 2006), although this has not been reported in turritellines.

Observed trematode infection rates of *Turritella communis* vary from 1–16% and have been described as "high" (Rothschild, 1935; Wright, 1956; Stunkard, 1964), but much higher rates (up to 97%) are known in many other marine gastropods (Poulin & Mouritsen, 2003), so it is not clear how important such infections are for turritellines. Rothschild (1935) and Wright (1956) reported that males are infected at much higher rates than females. The generally accepted explanation for this pattern is that the male gonad is active throughout the year and is therefore a more consistent host tissue for the parasite (Rothschild, 1935; Wright, 1956: 26).

TABLE 5. Parasites known to infect living turritellines.

Parasite higher taxon	Parasite species	Turritelline species	Notes	Reference
Gregarines (apicomplexan protists)	?	*T. communis*		Trégouboff (1918)
Trematodes (Platyhelminthes, Digenea)	*"Cercaria" rhodometopa*	*T. communis*	in gonads	Pérez (1924); Rothschild (1935); Hansson (1998)
	"Cercaria" pythionike	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" doricha	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" doricha-pigmentata	*T. communis*		Wright (1956)
	"Cercaria" nicarete	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" herpsyllis	*T. communis*	in gonads	Rothschild (1935); Hansson (1998)
	"Cercaria" turritellae	*T. communis*	in gonads and digestive gland	Hutton (1955); Hansson (1998)
	"Cercaria" ampelis	*T. communis*		Rothschild (1935)
	"Cercaria" ranzii	*T. communis*		Rothschild (1935)
	"Cercaria" cooki	*T. communis*		Wright (1956)
	Cercaria caribbea XVIII	*T. exoleta*		Martorelli et al. (2008)
	Cercaria melanocrucifera	*T. attenuata*		Reimer & Anantaraman (1968)
	Cercaria kuwaitae VII	*T. exoleta*		Abdul-Salam & Sreelatha (1996)
	unidentified	*Vermicularia spirata*	gonads	Bieler & Hadfield (1990)

Several species of pyramidellid gastropods have also been reported as parasitic on *Turritella communis* in the northeastern Atlantic (Table 5). Not all of these reports, however, may actually represent parasitism. As noted by Robertson & Mau-Lastovicka (1979), observations of associations in the field, and even animals in "feeding positions" in the lab, do not prove parasitism; feeding has to be seen and the parasite and host must be known to occur naturally in the same habitat. Smart (1887) reported "*Odostomia pallida*" (= *Brachystomia eulimoides* [Hanley, 1844]) "on the operculum" of *T. communis*; he did not mention feeding, but did note that the pyramidellids were withdrawn deeply into the shell with the operculum. Unaware of Smart's short paper (Ankel & Christensen, 1963:21), Ankel (1959) documented in detail parasitic feeding of "*Odostomia ambigua*" (= *Brachystomia eulimoides*) on *T. communis* in the laboratory, but the two can live in different habitats. Barnes (1994: 128) stated that *Brachystomia eulimoides* is "A common micro-predator of … *Turritella*…", presumably referring to parasitism, but he gave no reference or other information. Ankel (1959: 16–17) also observed *Brachystomia albella* on *T. communis* in the lab for 10 hours but he did not see it. Minichev (1971) observed "*Odostomia*" *fujitanii* actually feeding on *Turritella fortilirata* in the lab, but again the two species may not naturally co-occur in the same habitat. Køie (1989: 361) stated that in the western Kattegat off Denmark, "*O. eulimoides* parasitizes … *Turritella communis*", but it is not clear that this was based on any new observations.

Commensals and Epibionts

Living turritellines are known to host a large diversity and abundance of commensals and epibionts. The limpet *Capulus ungaricus* Linnaeus, 1758, for example, is commensal on *Turritella communis*, attaching to the shell inside the aperture of its living host, apparently without harming it (Thorson, 1965). Another patelliform gastropod, *Crucibulum quiriquinae* Lesson, 1830, attaches to the outside of the shells of living *T. cingulata* in Chile (Véliz et al., 2001). At least one species of hydroid, *Leuckartiara octona* Fleming, 1823, is found frequently on living and dead shells of *T. communis*, with two forms of the species occurring on different parts of the living snail (Rees, 1967). At least some of these hydroids capture emerging cercariae of the trematode *Renicola* (Wright, 1956: 38).

After the death of the snail, turritelline shells are frequently inhabited by hermit crabs (Paguridae) (Walker, 1992; Manjón-Cabeza & Raso, 1999; Barria et al., 2006), and other epibionts are frequently associated with these hermited (or "pagurized") shells. The cheilostome bryozoan *Hippoporidra senegambiensis* (Carter, 1882), for example, is frequently found on shells of *Turritella annulata* Kiener, which are inhabited by the pagurid *Diogenes ovatus* Miers, 1881 (Bassindale, 1961; Cook, 1964). The bryozoan *Lepralia edax* (Busk, 1859), which encrusts both gastropod and bivalve shells, dissolving the shell of the host and replacing it with its own construction (Hincks, 1880), has been reported on turritellines (Hyman, 1967: 381). Other hermit-associated epi- or endobionts on turritellines include bryozoans, corals, hydroids, spionid worms, sponges, and calcareous algae (Scott, 1885; Walker, 1992, 1998; van Soest, 1993). Empty turritelline shells may also be inhabited by other animals besides hermit crabs. The sipunculid *Phascolion strombi* (Montagu, 1804) frequently inhabits empty shells of *T. communis*, and is itself parasitized by the pyramidellid gastropod *Menestho diaphana* (Jeffreys, 1848) (Kristensen, 1970; Gibbs, 1978).

Abundance

Although they occur at various densities, high abundance or "gregarious habit" has long been cited as characteristic of turritellines, both in modern and fossil assemblages, and some occurrences of modern turritellines are among the most abundant reported for any large marine gastropod (Allmon, 1988; Table 6). The frequently high abundance of *Turritella communis* led Petersen (1913) to recognize it as a diagnostic component of benthic communities in waters off Denmark, and Petersen's work led Powell (1937) and Thorson (1957) to recognize "ecologically parallel" turritelline-dominated communities in New Zealand and Japan, respectively. Similar turritelline-dominated assemblages have been reported from the Mediterranean (Giacobbe & Mondello, 1994; Panetta et al., 2003).

High abundance of turritellines in fossil assemblages is so frequent that informal geological terms such as "Turritella-rock" (not to be confused with "Turritella agate"; see Allmon, 2009) are regularly used to describe them (Allmon, 1988, 2007). Allmon (2007: 513) defined a "turritelline-dominated assemblage" as "a macrofaunal assemblage in which turritelline gastropods (1) comprise either at least 20% of the total actual or estimated biomass or at least 20% of the macroscopic individuals in

TABLE 6. Reports of high density of living turritelline species (see also Allmon, 1988: table 2).

Species	Locality	Density/m^2	Reference
Maoricolpus roseus	Tasmania	> 1500	Probst & Crawford (2008)
Zeacolpus pagoda	New Zealand	1000-3500	Hayward et al. (1981)
Turritella cingulata	Chile	4000	Gaymer & Himmelman (2008)

the assemblage, and (2) are at least twice as abundant as any other macroscopic species in the assemblage". The term "turritelline-rich assemblage" is used for an assemblage that does not fit these quantitative requirements but in which turritellines are still the most abundant species (Allmon, 2007).

As discussed above, in the geological record the facies distribution of abundant turritellines through time suggests that their pattern of modern environmental occurrence is not completely representative. Abundant turritellines do occur in carbonate rocks, but these occurrences are concentrated in the Cretaceous and Paleogene, whereas they occur in siliciclastic facies throughout the history of the group, Early Cretaceous to Recent. Turritellines have therefore clearly undergone evolutionary change in their range of environmental occurrence over time; specifically they have shifted the thermal and facies distribution of abundance since the early Paleogene (warm to cool, carbonate + clastic to almost exclusively clastic), even while they maintained their preference for high nutrient-flux conditions. This change in the group occurred between the Cretaceous/early Paleogene and later Paleogene/Neogene (see Allmon [2007] for further discussion).

The frequently high abundance of turritellines suggests that they may be an example of the "Allee effect" (Stephens et al., 1999; Courchamp et al., 2008; also known as "inverse density dependence" or, in fisheries science, "depensation"; Liermann & Hilborn, 2001), in which individuals of a species benefit from the presence of conspecifics. The phenomenon can be caused by the necessity of high density for reproduction, predator avoidance, or other critical function. Kennedy (1995) specifically suggested that high turritelline abundance might be an example of Allee effect, and Allmon (1992, 2001) suggested that dependence on high abundance might make turritellines especially vulnerable to fluctuations in primary productivity.

TAPHONOMY

Information from living turritellines leads to mixed recommendations for taphonomic interpretations of fossil turritelline assemblages. In situ modern turritelline populations consist, at least at high densities, of large numbers of both living and dead shells (Holme, 1950; Buchanan, 1958; Sartenaer, 1959; Petuch, 1976). Giacobbe & Mondello (1994) emphasized the difference between the large number of dead shells of *Turritella communis* and the small number of living shells and described a "*Turritella thanatofacies*" in the Mediterranean. Nicastro et al. (2009) found that, on the southeastern coast of Australia, dead shells of *Maoricolpus roseus* were well preserved but their density did not increase in surface sediments over time. Instead, periodic burial was "sufficiently frequent to prevent the accumulation of shells in biologically active surface sediments", and kept this invasive turritellid from having marked effect on the native benthic biota. Near Auckland, New Zealand, dead shells of *M. roseus* are also much more common on tidal flats than living individuals, and most dead shells are pagurized and encrusted with calcareous algae and other epibionts (W. Allmon and U. Smith, unpublished observations).

Obviously fragmented, bored, or current-worn shells have been interpreted as having been buried after a significant post-mortem time interval at the sediment surface (Schafer, 1972; Allmon et al., 1995), although biological processes, such as habitation by hermit crabs, may alter this relationship (Walker, 1998). Use of "life position" criteria is common in taphonomic studies of benthic marine invertebrates, but information from living turritellines makes assumptions about life position in fossil assemblages problematic. Walker (1998) examined epibionts encrusting the inner surfaces of the shells of Recent *Turritella gonostoma* in the northern Gulf of California. She noted that on these shells the distribution of epibionts could be used as indicators of life position. Shells that had been inhabited post-mortem by hermit crabs had similar endobionts in higher frequencies, with the addition of the characteristic spionid trace fossil *Helicotaphrichnus* (similar results were reported for shells of *T. terebra* in Indonesia by Lescinsky et al. [2002]). Empty shells also had extensive clionid sponge borings and were more likely to have drill holes from predatory gastropods. Thus, Walker (1998) concluded that endobiont infestation is not restricted to empty shells, nor is it necessarily a reliable guide for "time since death" for fossils.

CONCLUSIONS

This review of the natural history of turritelline gastropods highlights not only what we do know, but also what we do not. Details of soft anatomy have been described for a very small number of species, and we really have no idea about ranges of interspecific variation in most characters. Radulae in particular have been strangely neglected. Although we know a good deal about growth rates, we know virtually nothing about either the functional or developmental biology of the turritelline shell. We know the basic reproductive and larval biology of several species: most appear to have short-term planktonic (planktotrophic?) larvae, but at least one is a true brooder. At least one other employs spermatophores, but we are still guessing, however, about mode of fertilization and larval behavior in most species. We know nothing at all about larval settlement. We know very little about diet and rates of feeding in the wild. Although there is strong circumstantial evidence for occasional movement by individuals over distances of more than a few centimeters, we are almost totally ignorant of behavior in the wild. Although there is strong evidence for a positive correlation of abundance with available nutrients and/or primary productivity, this has not been examined quantitatively or experimentally. Although turritellines are clearly eaten by many predators, we know very little about their actual interactions with these predators in nature, which makes posing and testing hypotheses about the influence of predation on their evolution very difficult.

All biology begins with natural history; that is, with basic observations about organisms and how they interact with their environment. This is especially true of evolutionary biology. No amount of genetic sequencing will ever reveal where species live or how they behave or move or feed or mate or react to predators or competitors. We are largely ignorant of even the most basic natural history information for the vast majority of species. This means that no matter how much else we learn about them, we cannot adequately understand how they came to be as they are.

Compiling natural history information of the type presented here is now both easier and more difficult than ever before. It is easier to assemble already existing data from the literature via increasingly complete on-line resources and sophisticated search tools. It is more difficult in many cases, however, to make new observations because many organisms no longer live where and how they once did. Just as the "crisis in systematics" focuses on describing species before they become extinct, so the "crisis in natural history" must focus on recording what those species do in their biotic and abiotic environments before opportunities to observe them in nature are gone. Clearly much of this information should come from new field observations. Yet a great deal of valuable data is available in both unpublished observations and scattered throughout the existing literature. There is an enormous need to gather new data, to mine and organize old data, and to encourage students and amateur and professional colleagues to do the same.

ACKNOWLEGEMENTS

For information and/or discussion, I am grateful to Donald Dan, Graham Edgar, Rod Feldmann, Jonathan Hendricks, Austin Hendy, Patricia Kelley, Amy McCune, Paula Mikkelsen, Robert Poulin, Robert Robertson, Gary Rosenberg, Carrie Schweitzer, Paul Shin, Chris Vos, Richard Waite, Sally Walker, and Anders Warén. For comments on previous drafts of the manuscript, I am particularly grateful to Klaus Bandel, Rüdiger Bieler, Paula Mikkelsen, Gary Rosenberg, and Ursula Smith. Special thanks are due to Paula Mikkelsen and Elizabeth Petsios for assistance with radula extraction and imaging; to Elizabeth Petsios and Nadia Pierrehumbert for assistance with shell sectioning and imaging; to Rüdiger Bieler, Felicity McEnnulty, Elizabeth Petsios, Ursula Smith, and Chris Vos for providing images; and to Amie Patchen and especially Maya Weltman-Fahs for assistance with references and figures. This work has been supported in part by NSF grant EAR-0719642.

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Revised ms. accepted 2 June 2011

MALACOLOGIA, 2011, 54(1–2): 203–406

THE CAMAENID SPECIES OF THE KIMBERLEY ISLANDS, WESTERN AUSTRALIA (STYLOMMATOPHORA: HELICOIDEA)

Frank Köhler

Department of Environment and Conservation of Western Australia, Science Division, Wildlife Place, Woodvale WA 6026 and Australian Museum, Sydney; Postal Address: Australian Museum, 6 College St, Sydney NSW 2010, Australia;
frank.koehler@austmus.gov.au

ABSTRACT

The present paper provides a complete overview of the camaenid land snail fauna of the 22 largest islands along the Kimberley coast, northwesternmost Western Australia, which were surveyed between 2007 and 2010. These islands were found to harbour a total of 104 species (83 new) in 15 genera (5 new), including taxa described recently. Species were essentially delimited by means of comparative analyses of shells (size, shape, sculpture, colouration), genital anatomy (in particular penial anatomy), and genetic differentiation in a mitochondrial marker (partial 16S rRNA sequences). Additionally, the radular and jaw morphology of selected species was studied but found to provide little useful information for taxonomic purposes. Species of the following genera are treated: *Amplirhagada* Iredale, 1933 (22 species), *Carinotrachia* Solem, 1985 (2 subspecies), *Kimberleymelon* Köhler, 2010 (1 species), *Kimberleydiscus* Köhler, 2010 (1 species), *Australocosmica* Köhler, 2011 (6 species), *Kimboraga* Iredale, 1939 (4 species), *Xanthomelon* Martens, 1860 (1 species), *Globorhagada* Iredale, 1933 (8 species; the name *Globorhagada* being removed from synonymy of *Xanthomelon*), *Rhagada* Albers, 1860 (8 species), *Retroterra* Solem, 1985 (3 species), *Baudinella* Thiele, 1931 (5 species), *Setobaudinia* Iredale, 1933 (14 species), *Torresitrachia* Iredale, 1939 (17 species or subspecies). In addition, two new genera, ***Molema***, n. gen. (one species) and ***Kimberleytrachia***, n. gen. (12 species), are described. The taxa *Torresitrachia umbonis* Solem, 1979, *T. deflecta* Solem, 1979, and *T. crawfordi* Solem, 1979, are transferred to the new genus ***Kimberleytrachia***. Species previously assigned to *Damochlora* are transferred to *Setobaudinia*; the former genus name likely being a junior synonym of the latter. The following species are delimited differently compared to the latest available revisions: "*Xanthomelon*" (now: *Globorhagada*) *prudhoensis* (E. A. Smith, 1894); "*Damochlora*" (now: *Setobaudinia*) *rectilabrum* (E. A. Smith, 1894); "*Torresitrachia*" (now: *Kimberleytrachia*) *umbonis* (Solem, 1979); *Torresitrachia amaxensis* Solem, 1979; *T. bathurstensis* (E. A. Smith, 1894). Most species were found to be island endemics. The work increases the number of known camaenids in northwestern Australia considerably and highlights the region as significant hotspot of land snail diversity.

Key words: Camaenidae, Pulmonata, taxonomy, land snail diversity, endemism, island fauna.

INTRODUCTION

The ancient landscapes of the Kimberley region of Western Australia are unique not only for their rugged beauty and inaccessibility, but also for the incredible biodiversity they support. Land snails are a component of this biodiversity that has received relatively little attention compared to vertebrate groups. Nonetheless, earlier works uncovered a large diversity of land snail species particularly in the rainforests (Solem, 1979, 1981a, b, 1984, 1985a, b, 1988, 1989, 1991, 1997).

These pioneering works showed that the land snail fauna of northwestern Australia is dominated by members of one family, the Camaenidae. Camaenid snails have developed adaptations that enable them to occupy a range of habitats from tropical rainforests to near deserts. In the Kimberley, centres of high diversity appear to be the wetter coastal areas in the northwest, where rainforest patches, including vine thickets, are most common. Prior to the Kimberley Island Survey, 185 camaenid land snail species in 23 genera were known from the Kimberley and immediately adjacent areas of

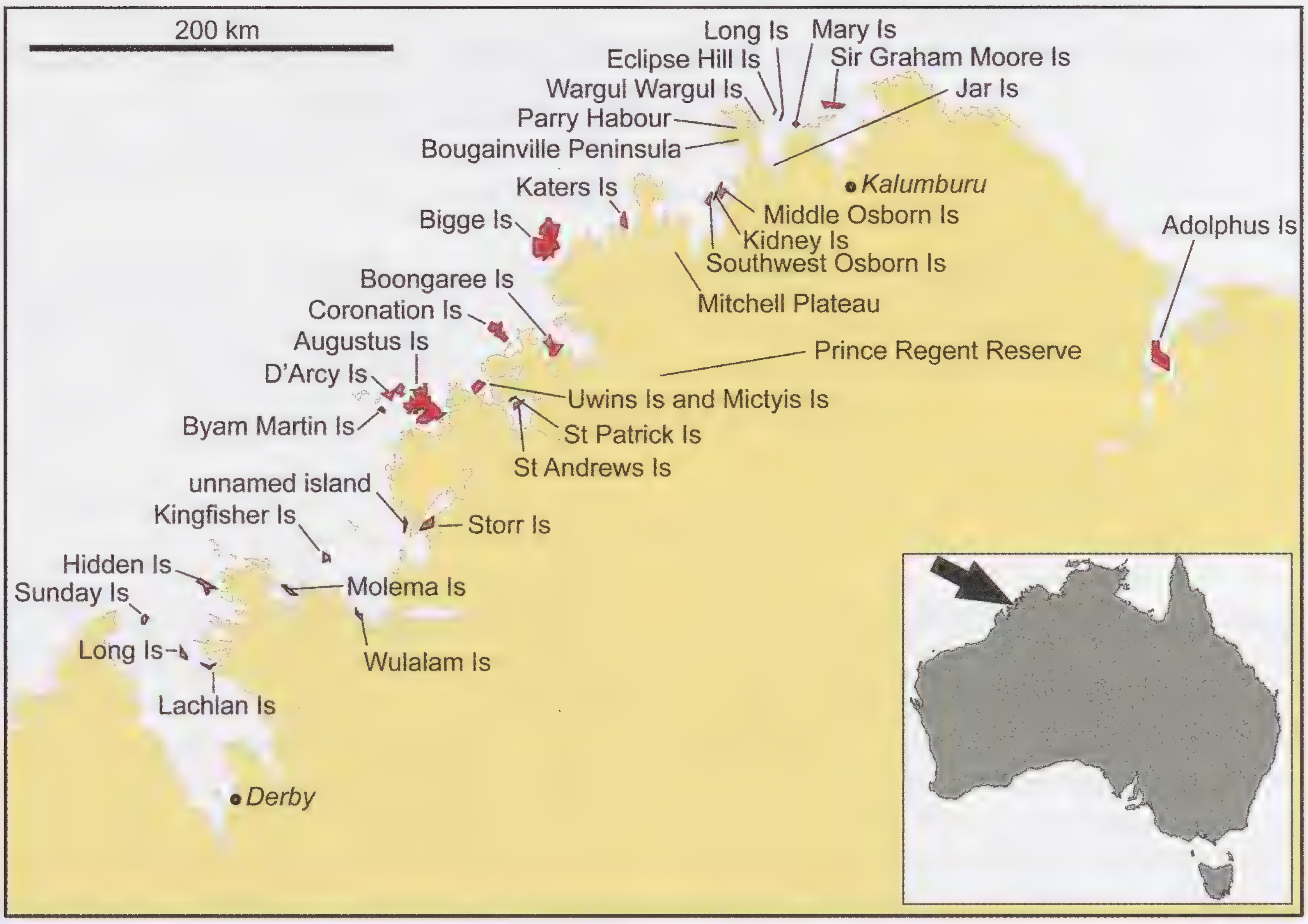


FIG. 1. Map of the Western Australian Kimberley with names of surveyed islands and other relevant localities.

the Northern Territory. This is the largest known regional diversity of camaenids in Australia. All species and almost all genera are endemic to the Kimberley region. In general, camaenid species have restricted geographic ranges, with an average range size on the mainland of no more than 20 square kilometres (Solem, 1991). Some species are even found on only a single rock outcrop, with a range diameter of mere metres (Willan et al., 2009).

Extensive archipelagos and island groups created by the drowning of an ancient coastline are found along the present day coast. There are hundreds of islands along the Kimberley coast, with 155 of them bigger than 100 hectares and 22 of more than 1,000 hectares. While these archipelagos represent much of the adjacent mainland's geology and vegetation types, the land snail fauna of most islands has widely remained unknown with usually only opportunistic reports being available.

From 2007 to 2010, a biodiversity survey was conducted on the largest islands by the Department of Environment and Conservation of Western Australia in collaboration with the Kimberley Land Council, the Western Australian Museum and the Australian Museum. Focussing on mammals, reptiles, frogs, birds, plants and land snails, this survey aimed to expand knowledge of biodiversity across the variety of islands.

While some taxonomic outcomes of the survey have already been published (Köhler, 2010a–c, 2011), the present paper provides a complete overview of the camaenid fauna of these islands along the Kimberley coast with emphasis on patterns of species diversity across the archipelagos and in comparison with findings for the mainland.

MATERIAL AND METHODS

Material

This account is based on ethanol preserved specimens and supplementary dry shell material collected during the Kimberley Island Survey (KIS) of the Department of Environment and Conservation, Western Australia (DEC) in 2007–2010. Voucher material and types are deposited in the Western Australian Museum, Perth (WAM), and the Australian Museum, Sydney (AM). Some additional samples from the Field Museum of Natural History, Chicago, Illinois (FMNH), were also studied. The location of the surveyed islands is shown in the map in Figure 1.

Field Work

Field work on the islands was conducted in survey teams with one person usually being responsible for snail collecting. Snails were collected in walking distance (i.e., < 3 km) of one or two collecting sites per island, which were carefully chosen by use of satellite images to ensure that different vegetation types and geological structures are covered. Emphasis was put on rainforest vegetation, including vine thickets, and gullies and gorges, being preferred by the snails for higher humidity. Each collecting site was visited twice a year by helicopter. In the dry season (May to August) sites were visited for five consecutive days and suitable habitats and structures (crevices in rocks, soil, leaf litter, rock piles etc.) were carefully searched for aestivating snails. All sites were visited again in the following wet season (February) for a single day. During this period of time snails were usually collected when being active.

Anatomical Studies

Samples from each collection site were initially sorted into morphotypes based on external shell morphology. Preliminarily identifications were based on comparisons with type material or topotypical material of known species. Comparative analyses of morphometric parameters of adult shells (recognised by complete lip) and features of the genital anatomy were employed to test whether operating units were correctly delimited and to confirm the preliminary determinations. Adult shell parameters were measured with a calliper precise to 0.1 mm. Parameters used were shell height (H = maximum dimension parallel to axis of coiling, including lip), shell diameter (D = maximum dimension perpendicular to H, including lip), width of umbilicus (U = diameter at half of total depth), height of last whorl (LW = maximum dimension from lower margin of aperture to upper suture delimiting the first whorl). The number of whorls (N), including protoconch, was counted precise to 0.1 as shown in Figure 2. The parameter "angle of mouth" describes the angle formed between aperture and the horizontal in degrees when the shell is in an upright position. The morphometric shell parameters H, D, LW, U, N, and H/D were subjected to morphometric analyses when considered necessary for the delimitation of species. Anatomy of genital organs was studied using a Leica M8 stereo microscope with drawing mirror. If not stated otherwise, the final inking of drawings was done by Martin Püschel (Sydney), some drawings of *Setobaudinia* were inked by Michael Shea (Sydney). Radulae and jaws were extracted manually, cleaned by soaking in 10% KOH solution for about six hours followed by rinsing in water and ethanol. They were mounted on carbon specimen tabs for electron scanning microscopy. Radular tooth formula gives the numbers of teeth as follows: C (central row of teeth) + number of lateral rows of teeth + number of transitional rows of teeth + number of marginal rows of teeth. Anatomy was studied from two (in small series) to five specimens per sample in order to confirm that observed features are consistently found among conspecific specimens.

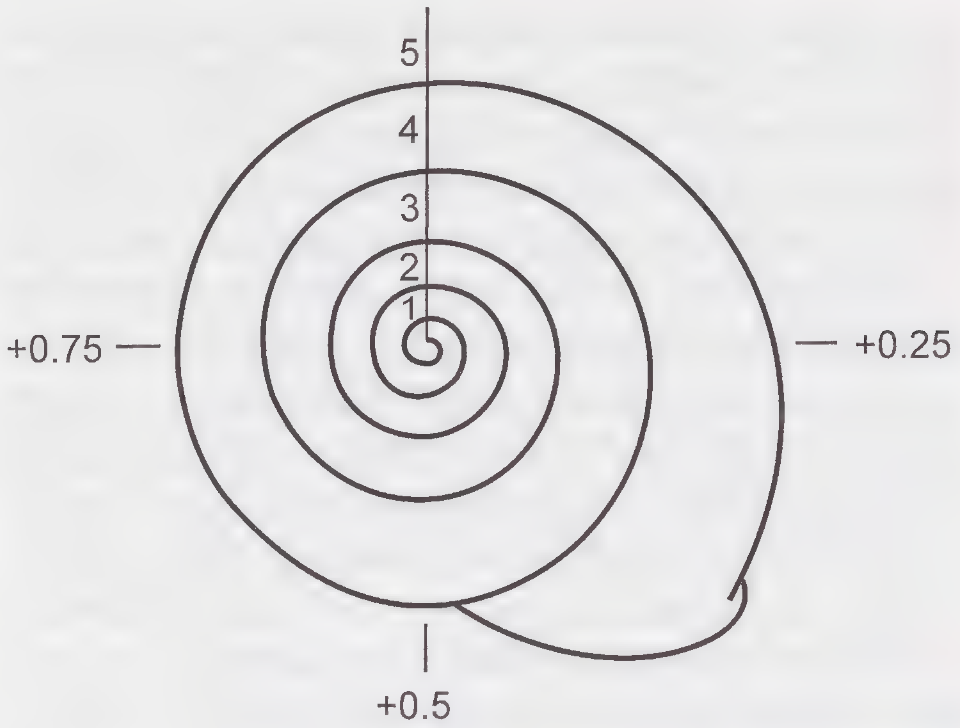


FIG. 2. Method of whorl count.

Clarification of Terms

For the description of shell features, in particular the microsculpture, terminology of Stanisic et al. (2010) is used. In verbal descriptions of the genital anatomy, with regard to the location of structures relative to each other, the terms "proximal" (= near) and "distal" (= far from) refer to the relative distance to the atrium, which sits anterio-ventrally, whilst the genital tract extends towards the posteriorly distal portion of the body. Hence, proximal and anterior as used herein are synonymous with each other as are distal and posterior.

In descriptions of features of the reproductive anatomy, Solem (1979, 1981a, b, 1984, 1985a, 1997) partly employed his own terminology, which has often been not consistent with the terms employed elsewhere. While Solem's terminology was widely followed by Köhler (2010a, b, 2011), here the attempt is made to be consistent with the general use of terms in land snail systematics. Solem referred to "prostate" (for prostate gland) and "uterus", terms that are widely used in land snail systematics. However, because both structures are fused in camaenids, instead the term "spermoviduct" is preferred here, which refers to the portion of the genital tract where prostate gland and uterus are fused with each other. Clarification of the term "spermatheca" as employed by Solem for Australian camaenids and subsequently followed by Clark (2009) and Köhler (2010, 2011) is required. In general, "spermatheca" refers to an organ in which allospermatozoa are stored and kept viable after copulation. Therefore, a spermatheca is identical with a seminal receptacle. However, in camaend snails the structure for which the term "spermatheca" was employed by Solem and others is a gametolytic gland but not a sperm-storing organ (Thompson & Bebbington, 1969; Brandriff & Beeman, 1973). Thus, the more widely used and correct term "bursa copulatrix" is applied instead (see also Barker, 1999: 27).

Frequently, the way how the epiphallus or the vas deferens (when a well-differentiated epiphallus is not present) opens into the lumen of the phallus is a characteristic feature. In some taxa, the vas deferens or epiphallus opens through a tubular penial verge, which is termed "verge". In other taxa, this vergic papilla is reduced in size (i.e., forming a "vergic ring") (Barker, 1999: 27). Instead of "epiphallic caecum", a term employed by Solem (also referred to as "epiphallus appendix" [sic!] by Jordaens et al., 2009), the most widely used term is actually "epiphallic flagellum" (e.g., Duncan, 1975; Tompa, 1984; Clark, 2009; Jordaens et al., 2009), which is hence preferred herein. The "vagina" is the most proximal part of the female oviduct extending from the atrium to the branching between bursa copulatrix and oviduct. The "free oviduct" is the part of the oviduct extending from the distal end of the vagina to the proximal end of the spermoviduct (uterus and prostate gland). The "anterior part of the oviduct" comprises vagina and free oviduct.

The development and relative size of some genital structures depends on the maturity of the animal and on its actual reproductive state. For dissection of genitalia, fully mature specimens (with adult shell features and fully developed albumen gland) were always chosen. However, amongst these specimens seasonal variation can be found with the genitalia being inactive and reduced in size in animals collected during the early to mid dry season (~ May to August) (Solem & Christensen, 1984). Because unavoidably the dissected specimens were collected at different times of the year, for each genital drawing the month of collection is given.

The following abbreviations are used:

ag	albumen gland
at	atrium
bc	bursa copulatrix
cl	corrugated lamellae
csw	connection of penial sheath and penial wall
ct	connective tissue
ef	epiphallic flagellum
el	epiphallic lobe
ep	epiphallus
epp	(longitudinal) epiphallic pilasters
fo	free oviduct
ft	foot
gr	sperm groove (of penial verge)
gu	gutter (on inner penial wall)
hd	hermaphroditic duct
hw	head wart
iw	inner penial wall
ll	lateral lamaellae
lp	longitudinal pilaster (of inner penial wall)
mp	main stimulatory pilaster (of inner penial wall)
op	oblique pilasters (of inner penial wall)
ov	opening to vas deferens (within epiphallus)
p	penis
pa	penis detached from atrium
pd	pad-like thickening of inner penial wall
pu	pustulation (of inner penial wall)
pv	penial verge
rm	penial retractor muscle
s	shell
sh	penial sheath
so	spermoviduct
tn	tentacle
vn	vagina
vd	vas deferens
vp	vergic papilla
vr	vergic ring

Molecular Work

DNA was extracted from small pieces of foot muscle by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. A fragment of the mitochondrial 16S rRNA gene (16S) was amplified by PCR using the primers 16Scs1 (Chiba, 1999a) and 16Sbd1 (Sutcharit et al., 2007). Reactions were performed under standard conditions with an annealing step of 90 s at 55°C. Sequences were aligned by use of the on-line version of MAFFT (Katoh et al., 2002) available at http://mafft.cbrc.jp/alignment/server/ using the "E-INS-I" strategy and standard parameters. The aligned sequence data set comprised 304 sequences and was trimmed to a total length of 827 bp. The sequence data was used to calculate uncorrected pair-wise genetic p-distances with the software MEGA 4.0 (Tamura et al., 2007) under the option "pair-wise deletion of gaps" in order to estimate the genetic differentiation of taxa. A phylogenetic analysis of mitochondrial sequences was not performed herein because a more complete phylogeny of the Western Australian Camaenidae under preparation is due to be published elsewhere. However, all taxa delimited herein by their morphology form monophyletic clades in mtDNA phylogenies based on analyses of 16S Köhler (2009, 2010c, unpublished data).

SYSTEMATIC PART

Within genera, species are listed in a north-south order of their occurrence along the Kimberley coast.

Gastropoda
Heterobranchia
Stylommatophora
Helicoidea Rafinesque, 1815
Camaenidae Pilsbry, 1895

Taxonomic Remarks

Delimitation of the Camaenidae is controversial. It has essentially been defined by lack of a dart apparatus (Pilsbry, 1939), a character state demonstrated likely to be plesiomorphic (Scott, 1996; Wade et al., 2007). Here, I follow Shileyko (2003) and Bouchet & Rocroi (2005) with regard to delimitation of the family (i.e., excluding New World taxa), but remark that the Camaenidae as so delimited remain non-monophyletic with respect to the Bradybaenidae, which possess a dart apparatus. Typical characters as given here for the family apply to Australian Camaenidae only, which are nested within a large camaenid-bradybaenid radiation (Wade et al., 2007; Hugall & Stanisic, 2010). All subfamiliar treatments previously suggested are not well supported by available phylogenetic data and are therefore in need of critical revision (Hugall & Stanisic, 2011).

Diagnosis

Australian helicoid taxa with variable shell, widely to narrowly winding umbilicus that may be partly to completely concealed by columellar reflection, undivided sole, elongate kidney, lacking dart apparatus, penial glands, diverticulum of bursa copulatrix, perivaginal glands and atrial appendix; uterus and prostate fused forming spermoviduct; inner wall of vagina, anterior oviduct and spermatophore with longitudinal pilasters; albumen gland elongate; talon simple, embedded within proximal part of albumen gland, sitting laterally. Hermaphroditic duct tightly undulating. Radula rectangular in shape; central teeth with triangular mesocones, tiny or vestigial ectocones; lateral teeth with triangular mesocones, tiny to vestigial ectocones and endocones; marginal teeth multicuspid, mesocones and endocones similar in length, ectocones smaller than endocones, occasionally subdivided.

Amplirhagada Iredale, 1933

Amplirhagada Iredale, 1933: 52; Solem, 1981a: 147–320; 1985a: 935–938; 1985b: 143–136; 1988: 28–32; 1991: 187–202; Solem & McKenzie, 1991: 247–263; McKenzie et al., 1995: 251; Johnson et al., 2010: 141–153; Köhler, 2010a: 217–284. Type species *Helix* (*Hadra*) *sykesi* E. A. Smith, 1894, by original designation.

Tenuigada Iredale, 1939: 68. Type species *Tenuigada percita* Iredale, 1939, by original designation.

Diagnosis

Shell: Medium sized (D = 15–30 mm; Table 1), thin (translucent) to moderately thick, broadly conical to dome- or beehive-shaped, moderately to strongly elevated; umbilicus narrowly winding, completely concealed to (rarely) entirely open; protoconch with very weak to strong, radially elongated pustulation; teleoconch sculptured by faint radial growth lines to well-developed radial ribs, ribs becoming oblique on base of shell; whorls rapidly increasing, separated by shallow to moderately deep suture; periphery well rounded to angulated. Shell colour variable, background often yellowish brown to horn, frequently banded, with brown subsutural and peripheral bands, or more rarely uniform.

Radula: 3.5–5.5 mm long, with 120–170 rows of teeth, C + 12–20 + 3–4 + 15–22.

Genital anatomy: Penis with well-developed sheath, extending entire length, usually thick proximally, thin distally; inner penial wall sculpture varying from smooth to heavily sculptured; epiphallus absent or wanting; penial retractor

TABLE 1. Shell parameters of *Amplirhagada*. Given are maximum – minimum (mean ± standard deviation) of shells for N measured specimens. Abbreviations used: HT = holotype, PT = paratype. Note that the method of whorl count differs from that applied by Köhler (2010b), who excluded the protoconch.

Species	N	Height (H)	Diameter (D)	Height of Last Whorl (LW)	Umbilicus (U)	No. of Whorls	H/D Ratio
A. euroa	13	12.3–13.9	18.5–20.3	9.6–11.0	chink	4.6–4.9	0.62–0.70
		(13.0 ± 0.5)	(19.6 ± 0.4)	(10.4 ± 0.4)		(4.8 ± 0.1)	(0.66 ± 0.02)
A. burrowsena	28	14.0–19.8	18.9–23.6	8.5–11.0	0–2.5	4.7–5.8	0.68–0.86
		(16.1 ± 1.3)	(20.7 ± 1.2)	(9.6 ± 0.5)		(5.4 ± 0.3)	(0.78 ± 0.05)
A. solemiana	20	9.9–12.2	16.2–18.4	8.3–10.0	0–1.0	4.0–5.1	0.59–0.69
		(11.2 ± 0.6)	(17.6±0.6)	(9.3±0.4)		(4.6±0.3)	(0.63±0.03)
A. indistincta	35	11.4–16.6	18.5–21.2	7.9–12.7	close-chink	4.2–5.0	0.58–0.81
		(13.8 ± 1.2)	(19.7 ± 0.7)	(10.1 ± 1.5)		(4.6 ± 0.2)	(0.70 ± 0.05)
A. katerana	45	12.8–20.9	19.3–25.0	10.0–14.2	chink to narrow	4.3–5.6	0.60–0.84
		(15.9 ± 1.8)	(22.1 ± 1.5)	(11.9 ± 1.0)		(5.0 ± 0.3)	(0.72 ± 0.06)
A. decora	23	14.8–20.6	18.2–22.0	10.4–14.4	close	3.5–4.7	0.79–1.04
		(17.8 ± 1.4)	(19.9 ± 0.9)	(12.6 ± 0.8)		(4.3 ± 0.3)	(0.89 ± 0.06)
A. kessneri	16	9.7–14.9	15.0–21.6	6.7–8.5	0–2.5	4.0–5.0	0.61–0.71
		(12.4 ± 1.4)	(19.0 ± 1.8)	(7.6 ± 0.5)		(4.6 ± 0.3)	(0.65 ± 0.03)
A. boongareensis	28	15.1–22.8	18.9–21.9	8.1–12.9	close-chink	4.5–6.8	0.80–1.12
		(20.0 ± 1.8)	(20.6 ± 0.8)	(9.4 ± 1.2)		(6.0 ± 0.6)	(0.97 ± 0.07)
A. gibsoni	16	12.0–14.9	17.1–19.2	6.4–10.6	chink	4.4–5.6	0.70–0.82
		(13.3 ± 0.7)	(18.1 ± 0.7)	(8.1 ± 1.4)		(5.2 ± 0.3)	(0.74 ± 0.03)
A. regia	20	14.5–18.2	21.8–26.0	11.4–14.6	close-chink	5.0–5.5	0.64–0.79
		(16.6 ± 1.0)	(23.4 ± 1.1)	(13.0 ± 0.7)		(5.3 ± 0.1)	(0.71 ± 0.05)
A. yorkensis	15	8.4–10.4	15.5–18.8	7.2–8.6	2.0–2.5	4.1–4.5	0.49–0.60
		(9.4 ± 0.6)	(17.3 ± 0.9)	(8.0 ± 0.4)		(4.3 ± 0.1)	(0.54 ± 0.03)
A. uwinsensis	23	14.3–17.1	20.0–23.2	11.3–13.2	close	5.8–6.4	0.66–0.76
		(15.6 ± 0.7)	(21.7 ± 0.8)	(12.2 ± 0.4)		(6.1 ± 0.2)	(0.72 ± 0.02)
A. sphaeroidea	8	13.5–15.8	20.9–23.0	11.1–12.9	close-chink	5.2–5.5	0.62–0.72
		(14.9 ± 0.7)	(22.0 ± 0.7)	(11.9 ± 0.5)		(5.3 ± 0.1)	(0.68 ± 0.03)
A. cf. *pusilla*	5	9.5–10.1	16.7–18.0	6.4–7.3	1.8–2.3	4.5–4.9	0.53–0.59
		(9.7 ± 0.2)	(17.6 ± 0.5)	(7.0 ± 0.3)	(2.1 ± 0.2)	(4.7 ± 0.2)	(0.55 ± 0.02)
A. globosa n. sp.	HT	13.8	20.4	7.9	chink	5.8	0.68
	16	13.8–15.4	18.4–20.6	7.1–8.0	chink	5.3–5.9	0.68–0.84
		(14.5 ± 0.5)	(19.4 ± 0.5)	(7.5 ± 0.3)		(5.6 ± 0.2)	(0.74 ± 0.03)
A. basilica	13	14.4–17.2	22.1–27.0	11.9–13.1	chink	5.1–5.4	0.56–0.73
		(15.7 ± 0.7)	(23.6 ± 1.2)	(12.6 ± 0.4)		(5.2 ± 0.1)	(0.66 ± 0.04)
A. camdenensis	11	14.8–17.3	18.7–19.8	11.1–12.3	0–2.5	4.8–5.3	0.78–0.89
		(16.2 ± 0.8)	(19.2 ± 0.4)	(11.6 ± 0.3)		(5.2 ± 0.1)	(0.85 ± 0.03)
A. sinenomine n. sp.	17	13.5–18.2	18.2–22.2	8.5–10.8	close	5.3–6.0	0.74–0.88
		(15.8 ± 1.3)	(19.7 ± 1.1)	(9.5 ± 0.6)		(5.6 ± 0.2)	(0.80 ±0.03)
A. storriana n. sp.	HT	18.3	21.0	9.5	chink	6.0	0.87
	24	16.1–20.0	19.8–22.5	8.2–13.5	chink	5.1–6.0	0.76–0.96
		(18.5 ± 0.8)	(21.2 ± 0.7)	(8.9 ± 1.1)		(5.7 ± 0.2)	(0.87 ± 0.05)
A. alkuonides n. sp.	HT	13.7	21.7	9.0	chink	5.5	0.63
	25	11.7–16.5	17.6–22.3	6.6–9.3	chink	5.0–5.9	0.60–0.74
		(13.7 ± 1.1)	(20.6 ± 1.1)	(7.9 ± 0.5)		(5.6 ± 0.3)	(0.66 ± 0.03)
A. cf. *astuta*	1	12.8	22.7	8.0	2.5	4.9	0.56

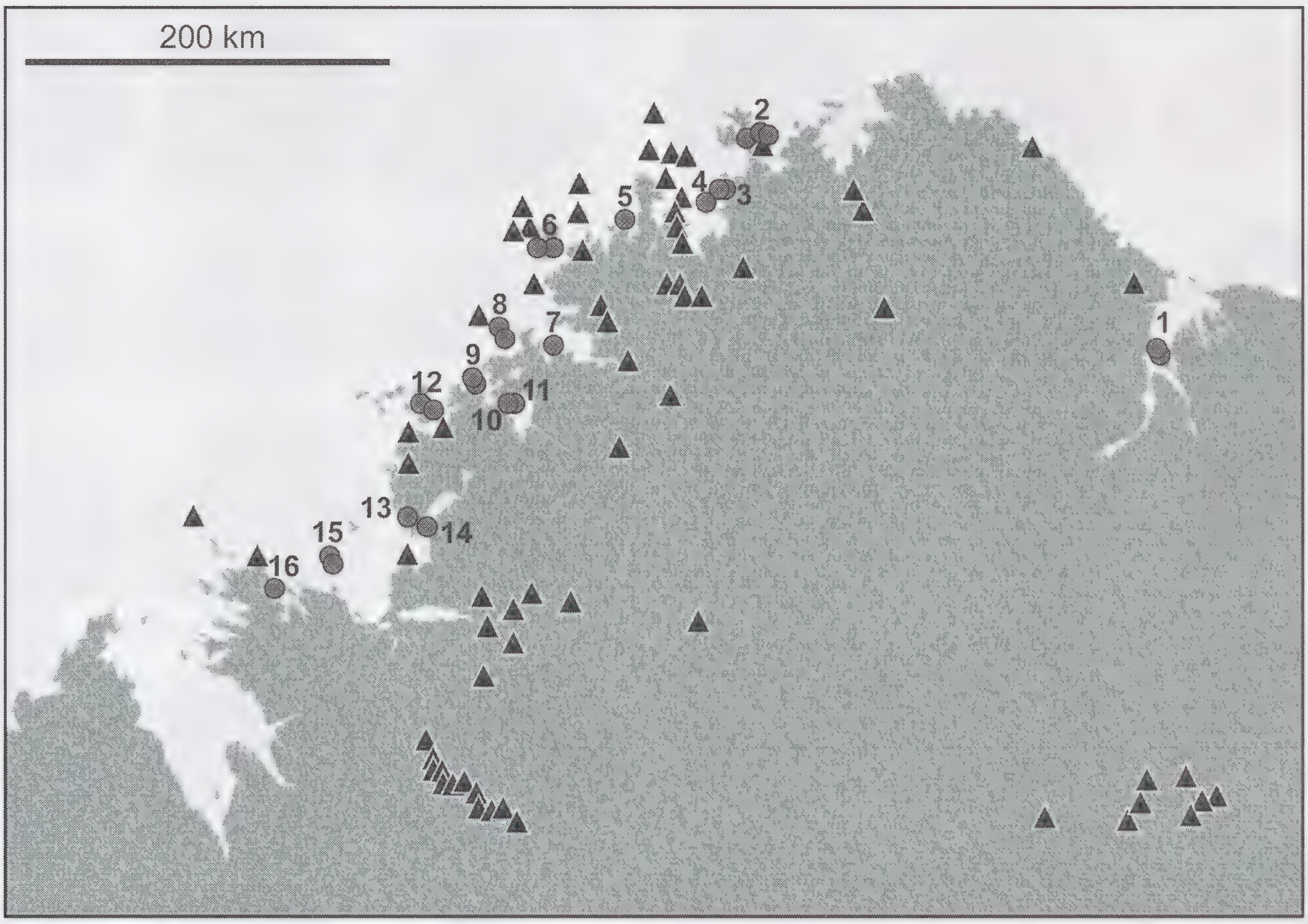


FIG. 3. Distribution map of *Amplirhagada*. Circles = Records of species treated herein: 1: *A. euroa* (Adolphus Island). 2: *A. burrowsena* (Bougainville Peninsula, Wargul Wargul and Eclipse Hill Islands, Vansittart Bay). 3: *A. solemiana* (Middle Osborn Island). 4: *A. indistincta* (Southwest Osborn and Kidney Islands). 5: *A. katerana* (Katers Island). 6: *A. decora* and *A. kessneri* (Bigge Island). 7: *A. boongareensis*, *A. gibsoni*, *A. regia* and *A.* sp. (Boongaree Island). 8: *A. yorkensis* (Coronation Island). 9: *A. uwinsensis* (Uwins and Mictyis Islands). 10: ***A. globosa*** n. sp. (St Patrick Island). 11: *A. sphaeroidea* and *A.* cf. *pusilla* (St Andrews Island). 12: *A. camdenensis* and *A. basilica* (Augustus Island). 13: ***A. sinenomine*** n. sp. (unnamed island in Doubtful Bay). 14: ***A. storriana*** n. sp. (Storr Island). 15: ***A. alkuonides*** n. sp. (Kingfisher and Melomys Islands). 16: *A. astuta* (Molema Island); triangles = Records of other congeneric species from the on-line catalogue of the Australian Museum.

muscle attached to junction with vas deferens. Vas deferens entering penial sheath halfway up to almost apically, entering penial chamber through verge. Bursa copulatrix simple, short (reaching or slightly extending anterior end of spermoviduct).

Aestivation Strategy

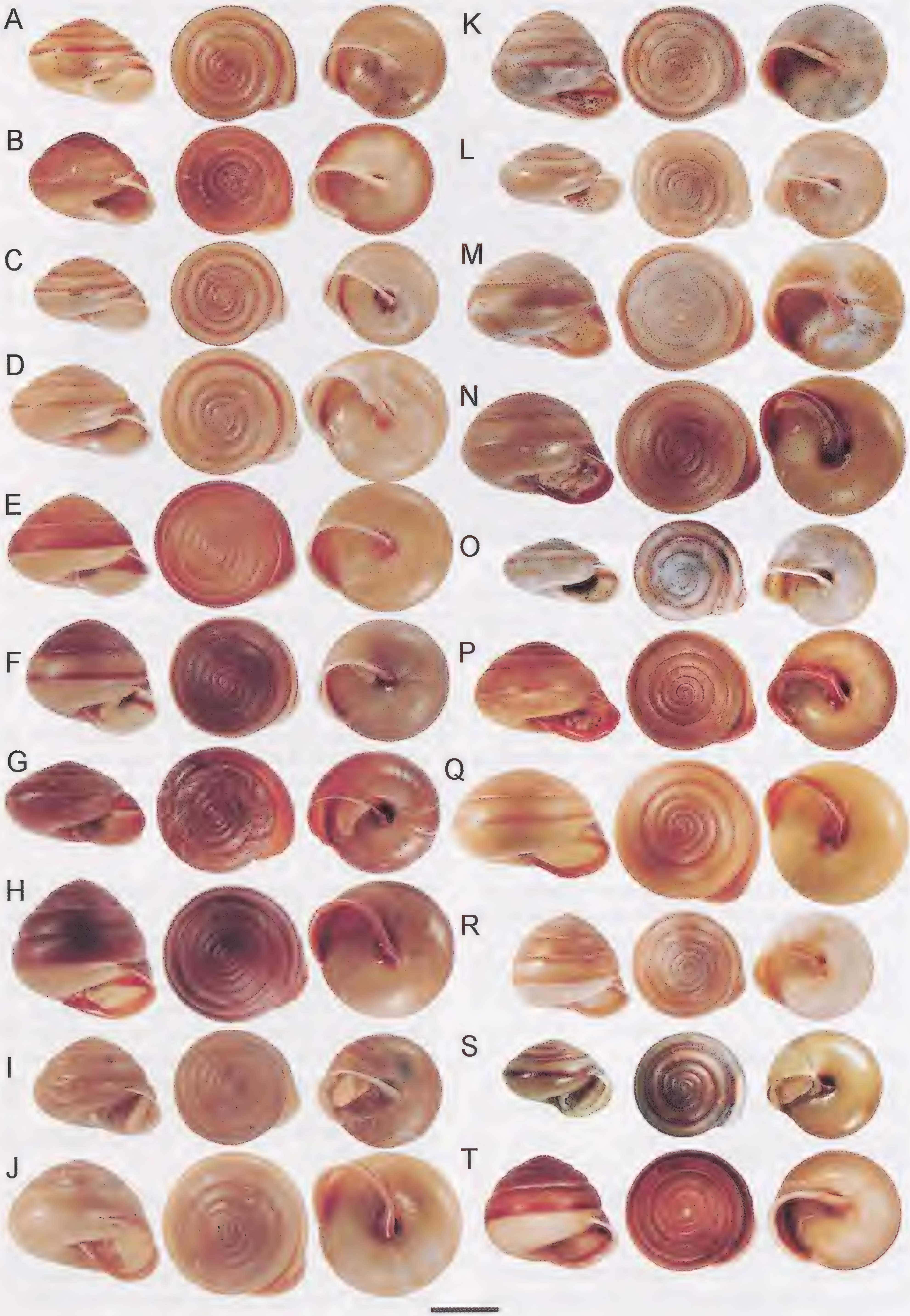
Rock or free sealer.

Taxonomic Remarks

Solem (1981a) provided the latest taxonomic revision and demonstrated that species are characterised particularly by penial features. Johnson et al. (2010) studied mitochondrial lineage differentiation (16S) of *Amplirhagada* populations across different islands in the Kimberley, which are not covered herein, showing that spatially isolated populations separated by distances larger than 10 km form clades, which are differentiated by genetic distances of 16–27%. Köhler (2010a) by comparing levels of anatomical and mitochondrial differentiation, demonstrated that comparable levels of genetic differentiation in COI are indicative of interspecific lineage differentiation. Accordingly, corrected pair-wise genetic distances (Tamura & Nei, 1993) ranged between 26 and 35% while infraspecific distances did not exceed 4%.

Diversity and Distribution (Fig. 3)

Amplirhagada is endemic to the Kimberley and arguably the most diverse camaenid genus in this region. Species are found along the coast within a distributional range from the Buccaneer Archipelago in the south to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Kalumburu in the north as well as in inland areas of the Napier, Oscar, Harding, and King Leopold ranges, the Drysdale River Reserve, Mt. Elizabeth Station and the region south of Wyndham (Solem, 1981a, 1988; Köhler, 2010a). Thirty species were described by 19th and 20th century authors, such as Smith (1894), Iredale (1938, 1939) and Solem (1981a, 1988), while an additional twenty-six species were recently described by Köhler (2010a) bringing the total species number to 56. This figure does not include four species described here nor some additional 15 species from rainforest patches across the Kimberley, which await formal description (F. Köhler, unpublished data).

Amplirhagada euroa Köhler, 2010
Figs. 4A, 5

Amplirhagada euroa Köhler, 2010a: 220–222, figs. 2–4.

Type Locality

Western Australia, eastern Kimberley, Cambridge Gulf, eastern section of Adolphus Island, 15°06’32”S, 128°09’08”E.

Material Examined

Holotype WAM S34601. Paratypes AM C463680 (6 preserved specimens, as holotype), WAM S37083 (12 preserved specimens) from type locality, WAM S37390 (3 shells) from 15°06’18”S, 128°09’04”E; WAM S37391 (shell) from 15°06’35”S, 128°09’57”E; AM C463680 (6 shells), WAM S37392 (11 shells) from 15°06’32”S, 128°09’08”E; WAM S37393 (3 shells) from northern Adolphus Island, 15°04’19”S, 128°08’18”E.

Diagnosis

Shell: Broadly conical with low to medium spire; umbilicus 50–90% concealed (Fig. 4A, Table 1); teleoconch sculptured by fine axial lirae; colour yellowish brown, with chestnut brown, thin to moderately broad, diffuse to well-defined subsutural and peripheral bands, clearly visible on last whorls only.

Genital anatomy: Penial verge short, less than 1/5 of length of penial chamber, slender with rounded tip. Penial wall pustules normal to elongated, arranged in rows over entire length of inner penial wall. Main stimulatory pilaster large, cone-shaped, comprising entire length of inner penial wall; sculptured by ridges with smooth, flattened pustules (Fig. 5).

Comparative Remarks

Geographically well separated from most other congeners; species occurring closest are *A. cambridgensis* Solem, 1988 (from western bank of Cambridge Sound), and *A. questroana* Solem, 1981 (from El Questro Station near Wyndham, ~ 100 km S of Adolphus Island). While shells are similar, *A. euroa* differs in penial wall pustules forming corrugated longitudinal pilasters; *A. questroana* differs by an open umbilicus and a shorter and corrugated main stimulatory pilaster.

Distribution (Fig. 3)

Eastern Kimberley, Cambridge Gulf, Adolphus Island.

←

FIG. 4. Shells of *Amplirhagada* species (continued in Fig. 39). A: *A. euroa* paratype WAM S37392 (Adolphus Island); B: *A. burrowsena* WAM S49320 (Wargul Wargul Island); C: *A. solemiana* paratype WAM S36572 (Middle Osborn Island); D: *A. indistincta* paratype WAM S36499 (Southwest Osborn Island); E: *A. katerana* WAM S36580 (Katers Island); F: *A. decora* holotype WAM S34609 (Bigge Island); G: *A. kessneri* holotype WAM S34610 (Bigge Island); H: *A. boongareensis* holotype WAM S34616 (Boongaree Island); I: *A. gibsoni* holotype WAM S34617 (Boongaree Island); J: *A. regia* holotype WAM S34615 (Boongaree Island); K: *Amplirhagada* sp. WAM S36953 (Boongaree Island); L: *A. yorkensis* paratype WAM S37401 (Coronation Island); M: *A. uwinsensis* paratype WAM S37441 (Uwins Island); N: *A. sphaeroidea* holotype WAM S34622 (St Andrews Island); O: *A.* cf. *pusilla* WAM S37405 (St Andrews Island); P: ***A. globosa*** n. sp. holotype WAM S58432 (St Patrick Island); Q: *A. basilica* holotype WAM S34623 (Augustus Island); R: *A. camdenensis* holotype WAM S34624 (Augustus Island); S: ***A. sinenomine*** n. sp. paratype WAM S37709 (unnamed island in Doubtful Bay; sub-adult). T: ***A. sinenomine*** n. sp. paratype WAM S37805 (unnamed island in Doubtful Bay; adult). Scale bar = 10 mm. Note that foot tissue protrudes from some shells.

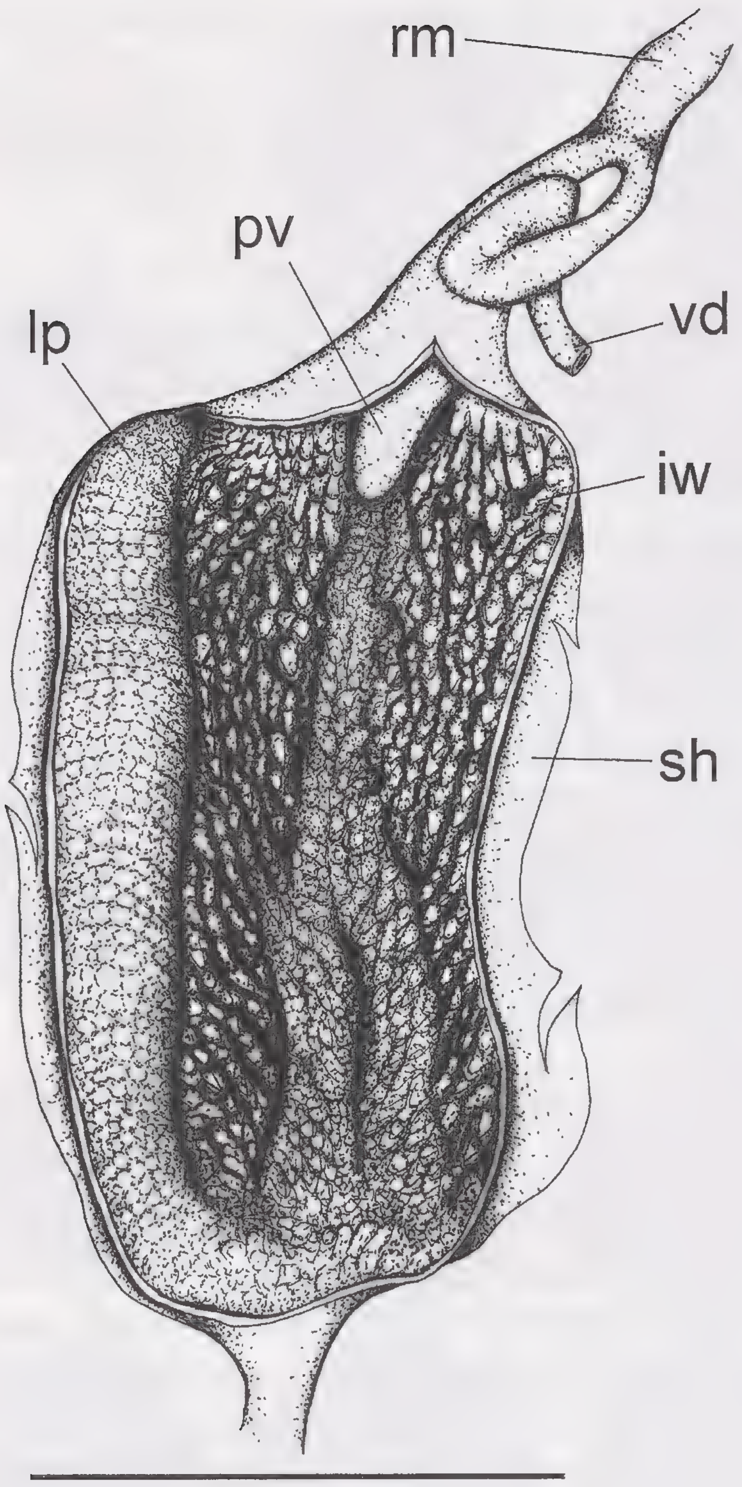

FIG. 5. Penial anatomy of *Amplirhagada euroa* (paratype AMS C463680, Adolphus Island; August). Scale bar = 5 mm.

Amplirhagada burrowsena Iredale, 1939
Figs. 4B, 6–8

Amplirhagada burrowsena Iredale, 1939: 68, pl. V, fig. 9 (Vansittart Bay, northwest Australia).
Amplirhagada imitata – Solem, 1981: 306–310 (partim).

Type Locality

Western Australia, northwestern Kimberley, Vansittart Bay.

Taxonomic Remarks

This species was named by Iredale (1939) based on three dried and worn shells from Vansittart Bay. It was subsequently treated as synonym of *A. imitata* (E. A. Smith, 1894) from Baudin and Condillac islands, Institute Islands by Solem (1981a) for having a similar shell. Solem (1981a) also designated the lectotype of *A. burrowsena* (AM C106525). He assumed that *A. imitata* has a comparatively wide distribution spanning various islands in the Admiralty Gulf and the adjacent mainland coast. This assumption was not based on comparative study of preserved material that would have permitted dissection. Preserved material from the type locality of *A. imitata* (Baudin Island) is still not available. However, Köhler (2010a) showed that islands in close proximity of Baudin and Condillac islands, such as Fenelon and Descartes islands, harbour distinct species (*A. montesquieuana* Köhler, 2010, and *A. descartesana* Köhler, 2010, respectively). Hence, localities in much larger distance are considered unlikely to harbour conspecific populations, which would render the distribution of this species remarkably disjunct. Consequently, the name *A. burrowsena* is removed from synonymy of *A. imitata*. The anatomy is described for the first time based on material from localities around Vansittart Bay.

Material Examined

Lectotype AM C106525 (dry and worn shell); additional, non-type material WAM S49351 (3 preserved specimens), WAM S49327 (42 shells), AM C471708 (10 shells) from Bougainville Peninsula, Vansittart Bay, 13°55’58”S, 126°08’53”E; WAM S49355, WAM S49357–8, WAM S49364, AM C471710 (4 preserved specimens), WAM S49320–6, AM C471709 (30 shells) from Wargul Wargul Island, Vansittart Bay, N Kimberley, 13°56’S 126°10E; WAM S49350 (8 preserved specimens), AM C471711 (10 shells), WAM S49328 (41 shells) from Eclipse Hill Island, Eclipse Archipelago, Vansittart Bay, 13°56’31”S, 126°17’01”E.

Description

Shell (Figs. 4B, 6; Table 1): Subglobose to broadly conical with moderately to highly elevated spire; thick to solid; periphery evenly rounded to slightly angulated; upper and basal sector of whorls well rounded. Umbilicus forming a chink (80–95% concealed), or completely concealed. Background colour whitish horn to yellowish brown, with well-defined to diffuse, moderately broad, subsutural and peripheral bands, usually visible on entire shell; ventral, outer and inner lip colour pale horn to white. Protoconch 2.3–2.7 mm in diameter, comprising one whorl, with comparatively strong axial ribs. Teleoconch with comparatively strong, regular

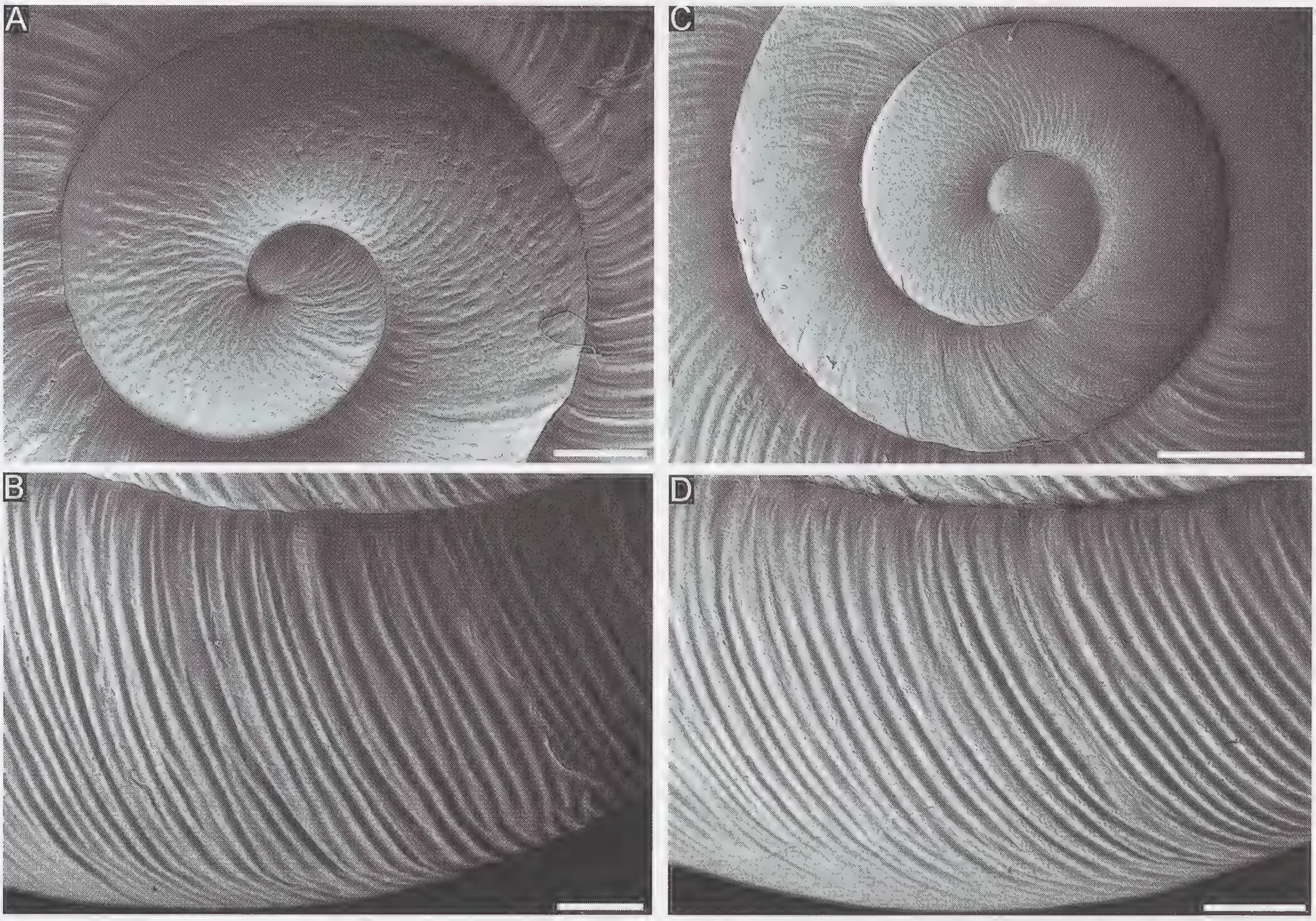

FIG. 6. SEM micrographs of the shell of *Amplirhagada burrowsena*. A–B: AM C471708, Bougainville Peninsula; A: Apical view showing protoconch, scale bar = 0.5 mm; B: Sculpture on last whorl, scale bar = 1 mm; C–D: AM C471709, Wargul Wargul Island; A: Apical view showing protoconch. Scale bar = 1 mm; B: Sculpture on last whorl. Scale bar = 1 mm.

lirae, rounded in cross-section, spaces equal to thickness of lirae, evenly distributed across whorls, height reduced underneath suture. Angle of aperture 30–45°, outer lip thickened, rounded, slightly to well expanded, slightly reflected, basal node usually strongly developed, parietal wall of inner lip inconspicuous.

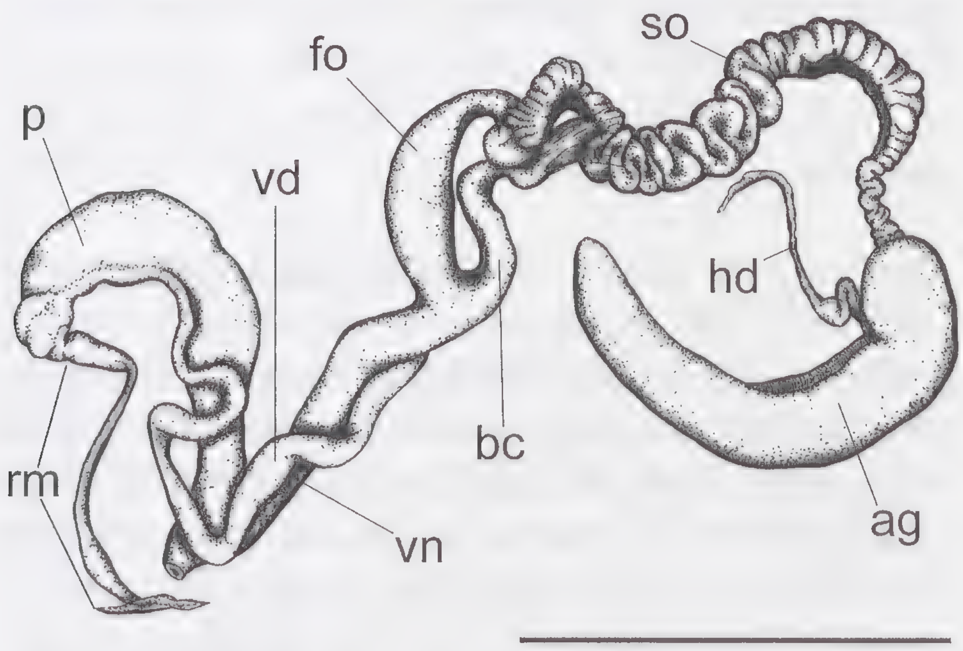

FIG. 7. Genital anatomy of *Amplirhagada burrowsena* (WAM S49355, Wargul Wargul Island; June). Scale bar = 10 mm.

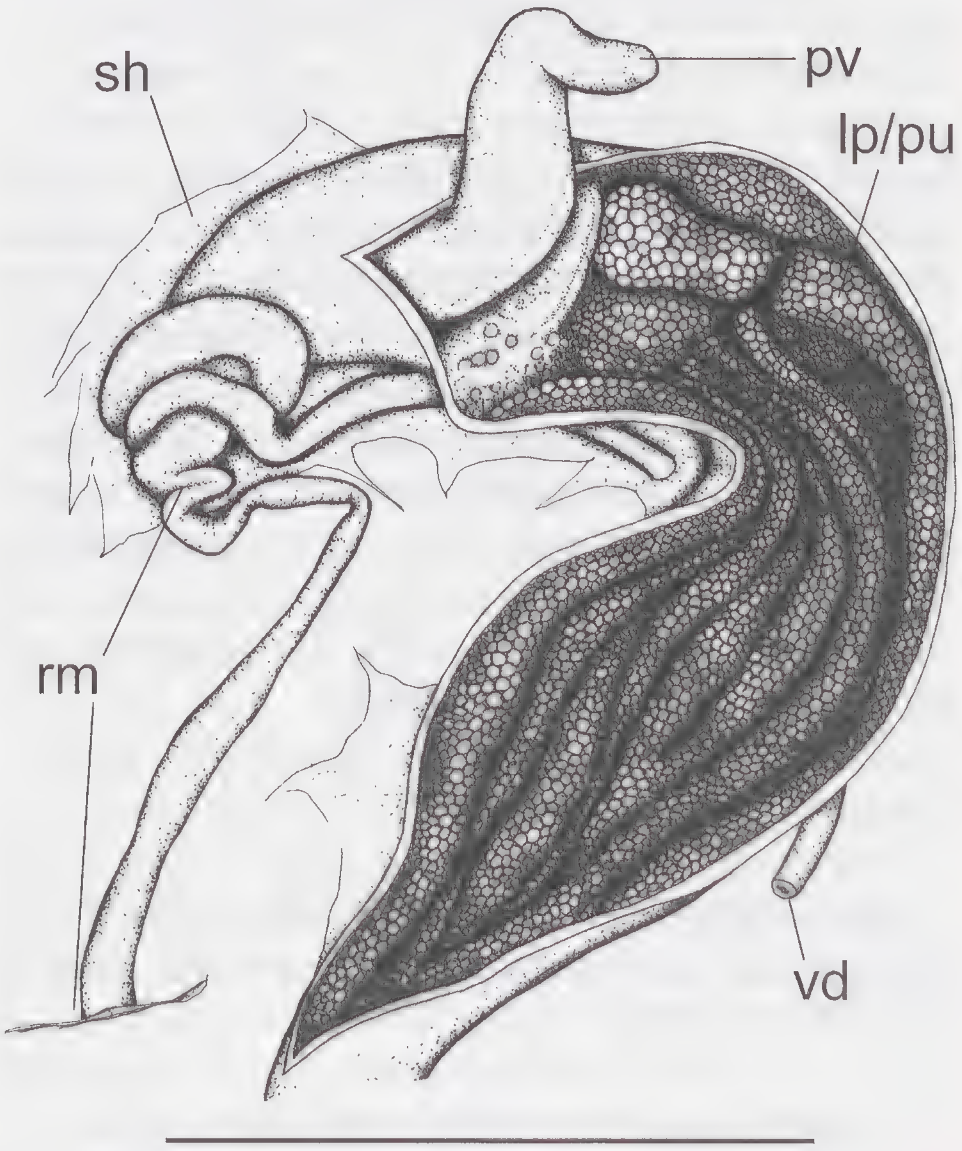

FIG. 8. Penial anatomy of *Amplirhagada burrowsena* (WAM S49355, Wargul Wargul Island; June). Scale bar = 5 mm.

Genital anatomy (Figs. 7–8): Penis curved, as long as anterior part of oviduct. Vas deferens entering sheath within distal third. Penial verge long to very long (~ 1/3 of penial chamber), broad with rounded tip. Inner penial wall sculpture comprising entire length except immediately adjacent to verge, penial wall pustules small to moderate in size, densely arranged in rows; numerous corrugated longitudinal pilasters are formed by partly fused rows of elevated pustules; main stimulatory pilaster not differentiated. Inner vaginal wall pilasters formed by minute, densely arranged pustules, weak to well developed.

Mitochondrial Differentiation

Distances between conspecific samples from two different islands (Wargul Wargul and Eclipse Hill islands) (3 sequences): 0.062–0.069; interspecific distances with respect to all other congeneric species (57 sequences, 33 species): 0.179–0.230.

Comparative Remarks

Amplirhagada imitata, *A. solemiana*, *A. indistincta* and *A. burrowsena* belong to a species complex, which based in similarity in shell features was considered as a single species, *A. imitata* by Solem (1981a). All aforementioned species have similar shells with respect to colour, shape and sculpture and also exhibit largely corresponding genital anatomy (with that of topotypic populations of *A. imitata* remaining unknown). Similarity of these species is considered to reflect common ancestry and/or parallel adaptation to nearly identical environments. Shells exhibit remarkable variability within local populations. However, some distinct features can be identified with respect to shell shape and size. Shells of *A. solemiana* and, to a lesser degree, of *A. indistincta* are more depressed and smaller than those of *A. burrowsena* and *A. imitata*. *Amplirhagada burrowsena* is removed from synonymy of *A. imitata* for reasons explained in taxonomic remarks.

Distribution (Fig. 3)

Northwestern Kimberley, Bougainville Peninsula, Wargul Wargul and Eclipse Hill Island in Vansittart Bay.

Amplirhagada solemiana Köhler, 2010
Figs. 4C, 9

Amplirhagada solemiana Köhler, 2010a: 222–225, figs. 5–7.

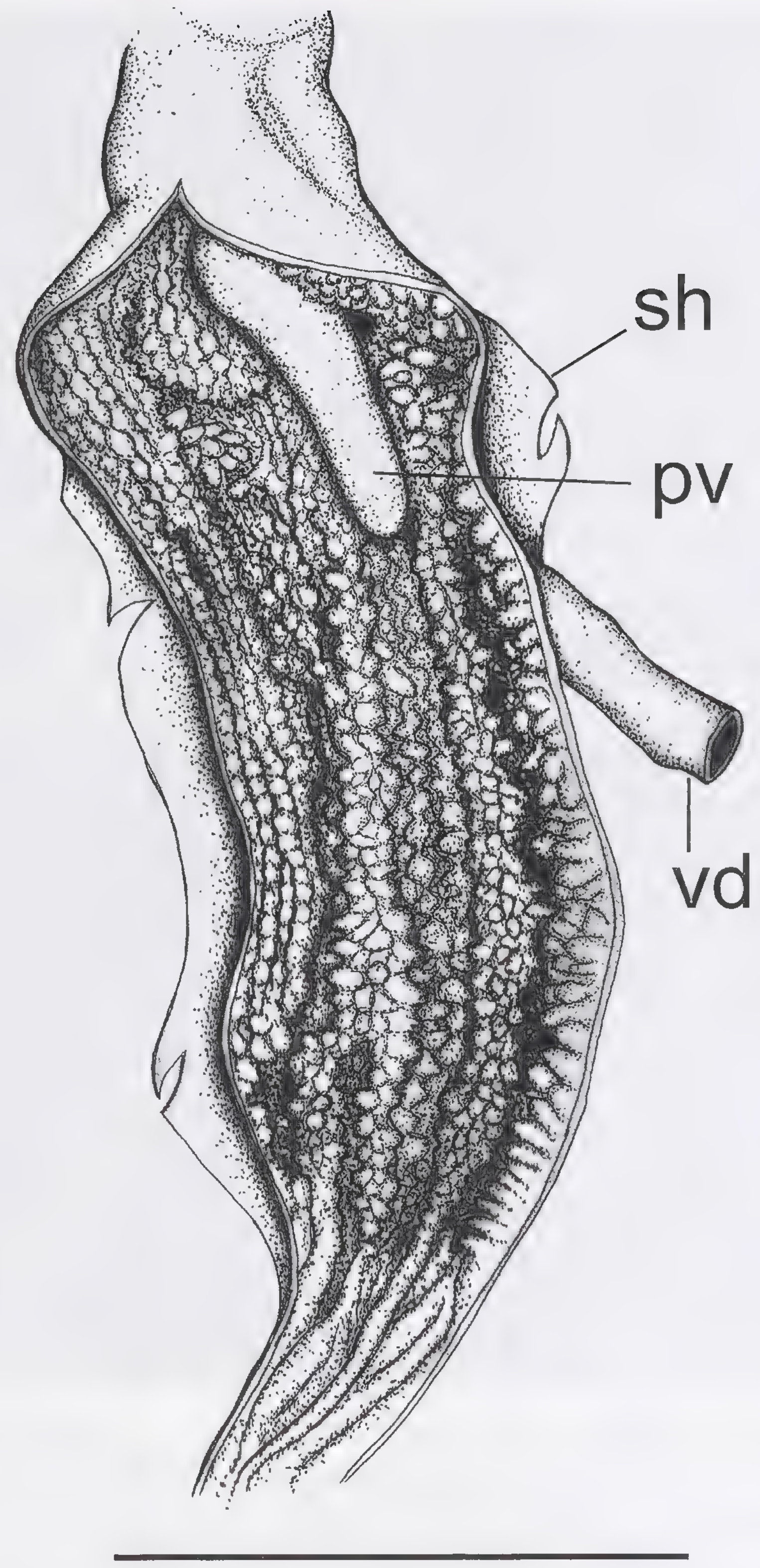

FIG. 9. Penial anatomy of *Amplirhagada solemiana* (AM C463681, Middle Osborn Island; February). Scale bar = 3 mm.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, W coast of Middle Osborn Island, 14°18’18”S, 125°59’35”E.

Material Examined

Holotype WAM S34602. Paratypes AM C463681 (8 preserved specimens), WAM S36860 (20 preserved specimens) from type locality; AM C463683 (4 shells), WAM S36572 (10 shells) from 14°18’37.4”S, 125°59’18.4”E; AM C463682 (2 preserved specimens), WAM S36589 (6 preserved specimens) from east coast, 14°18’53.5”S, 126°02’06.7”E. Additional, non-type material WAM S36471, WAM S36566–71, WAM S36573, WAM S36585–99, WAM S36858, WAM S36861, WAM S36971, AM C463684–5 from Middle Osborn Island.

Diagnosis

Shell: Subglobose with moderately high spire; periphery evenly rounded to slightly angulated; umbilicus 80–90% concealed; colour horn to yellowish brown, with brown, well-defined to diffuse, moderately broad, subsutural and peripheral bands, visible on entire shell; teleoconch sculptured by coarse, regular lirae (Fig. 4C, Table 1).

Genital anatomy: Penial verge long to very long (ca. 1/3 to 1/2 of penial chamber), slender to spatulate with pointed tip. Inner penial wall with pustulation along its entire length, pustules small to moderate in size, densely arranged in rows, some of which form four to five corrugated longitudinal pilasters; main stimulatory pilaster not differentiated. Inner vaginal wall pilasters formed by minute, densely arranged pustules, weakly to well developed (Fig. 9).

Comparative Remarks

Morphologically most similar are *A. indistincta*, *A. imitata* and *A. burrowsena* (see under *A. burrowsena*). Differs from *A. imitata* and *A. burrowsena* most considerably by smaller and more depressed shell.

Distribution (Fig. 3)

Middle Osborn Island.

Amplirhagada indistincta Köhler, 2010
Figs. 4D, 10

Amplirhagada indistincta Köhler, 2010a: 225–227, figs. 10–12.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, W coast of Southwest Osborn Island, 14°22’26”S, 125°56’13”E.

Material Examined

Holotype WAM S34603. Paratypes AM C463686 (5 preserved specimens), WAM S36617 (10 preserved specimens) from type locality; AM C463688 (5 shells), WAM S36575 (15 shells) from 14°22’26”S, 125°56’13”E; AM C463687 (20 preserved specimens), WAM S36865 (40 preserved specimens) from 14°22’26.5”S, 125°56’17.8”E; AM C463689 (11 shells), WAM S36962 (25 shells) from east coast, 14°22’47.3”S, 125°56’00.6”E. Additional, non-type material WAM S28521, WAM S36491–501, WAM S36574, WAM S36577, WAM S36612–16, WAM S36618–25, WAM S36863–4, WAM S36866, AM C463690–1 from Southwest Osborn Island; WAM S41454, AM C463724 from Kidney Island, 14.329 S, 125.985 E.

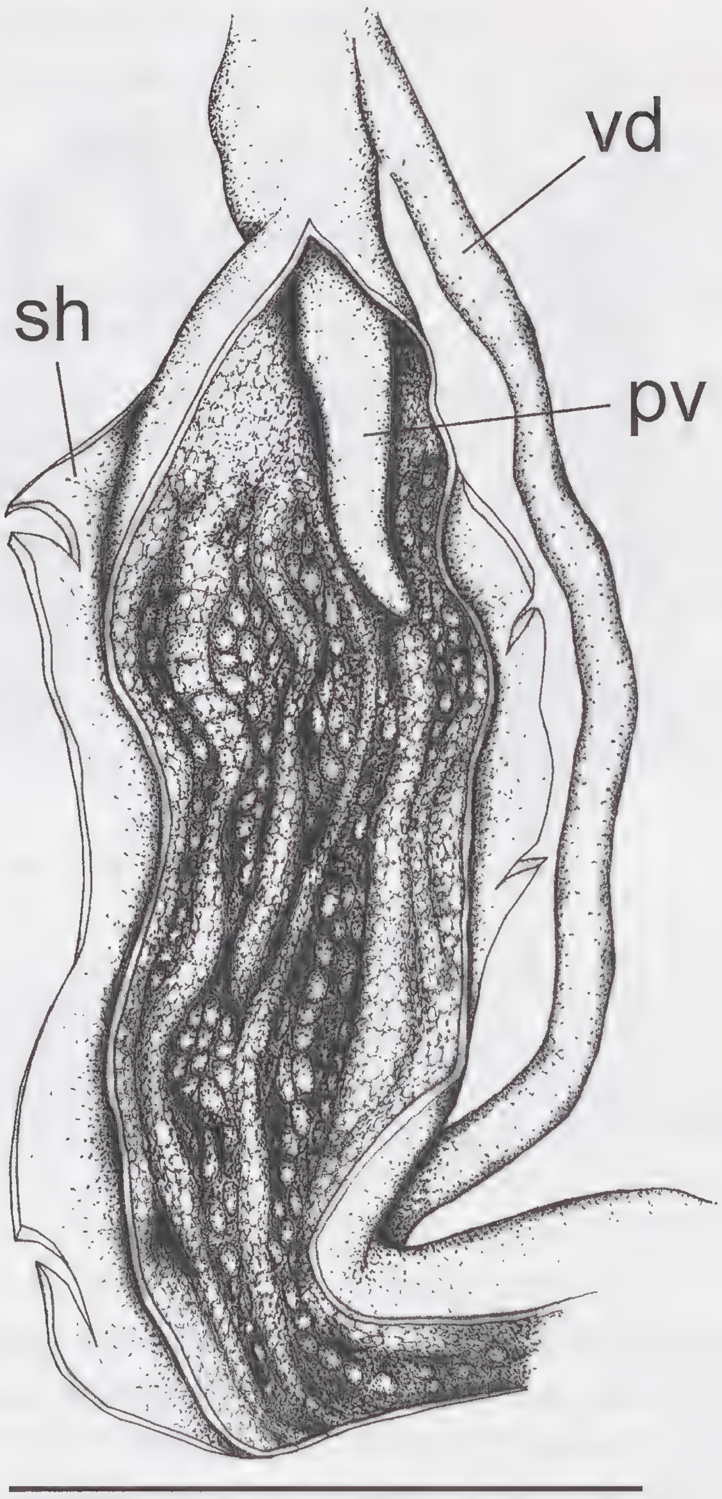

FIG. 10. Penial anatomy of *Amplirhagada indistincta* (AM C463687, Southwest Osborn Island; February). Scale bar = 5 mm.

Diagnosis

Shell: Subglobose to broadly conical with moderate to high spire; periphery well rounded to slightly angulated; umbilicus completely concealed. Background colour yellowish to brownish white, with thin to moderately broad brown to yellowish-brown subsutural and peripheral bands that are visible on most whorls, subsutural band diffuse, peripheral band well marked, ventral colour whitish to greyish white. Teleoconch sculptured by coarse, regular, in cross-section rounded

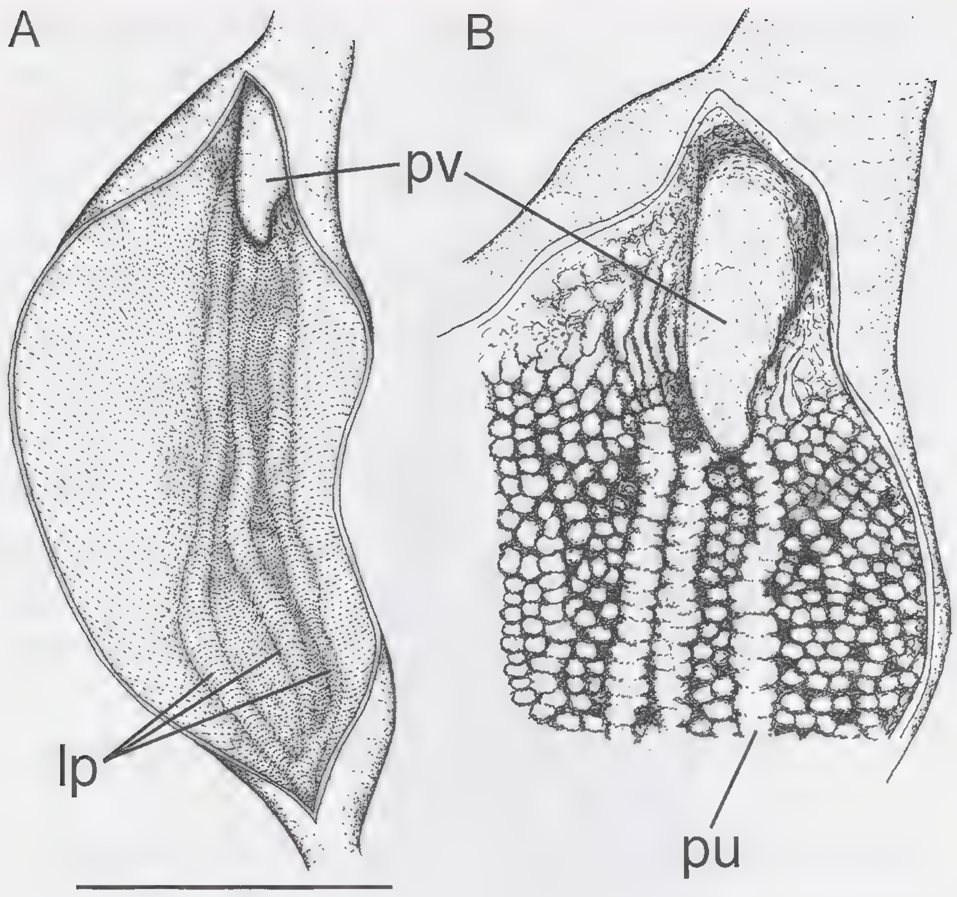

FIG. 11. Penial anatomy of *Amplirhagada katerana* (AM C463692, Katers Island; July). A: General overview of internal antomy. Scale bar = 5 mm; B: Magnification of pustulation.

lirae, spaces between lirae equal to thickness of lirae, height reduced underneath suture (Fig. 4D, Table 1).

Genital anatomy: Penial verge long to very long (ca. 1/3 to 1/2 of penial chamber), slender to spatulate with pointed tip. Pustulation comprising entire length of inner penial wall; penial wall pustules small to moderate in size, densely arranged in rows, some of which form four to five longitudinal pilasters along entire length of penial chamber; main stimulatory pilaster not differentiated. Vas deferens entering penial sheath apically. Inner vaginal wall pilasters formed by minute, densely arranged pustules, weakly to well developed (Fig. 10).

Comparative Remarks

Morphologically most similar are *A. solemiana*, *A. imitata* and *A. burrowsena* (see under *A. burrowsena*). Differs from *A. imitata* and *A. burrowsena* most considerably by more depressed shell, from *A. solemiana* by larger size. In addition, *A. solemiana* and *A. indistincta* are genetically well differentiated (Köhler, 2010a). Specimens from Kidney Island, which is located in between Middle and Southwest Osborn islands, have slightly larger and more robust shells than specimens from the type locality.

Distribution (Fig. 3)

Southwest Osborn and Kidney islands.

Amplirhagada katerana Solem, 1981
Figs. 4A, 11

Amplirhagada katerana Solem, 1981a: 198–201, figs. 37d, 41a, 43e, f; Köhler, 2010a: 236–238, figs. 27–29.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Montague Sound, Katers Island.

Material Examined

AM C463692, AM C463695–6, WAM S36601, WAM S36878–80 (preserved specimens) from Katers Island, 14°26'49–52"S, 125°31'07–15"E (Fig. 1).

Diagnosis

Shell: Subglobose; periphery evenly rounded to angulated; umbilicus forming 80–95% concealed. Background colour horn, with diffuse to well-marked, dark brown, moderately to very thick subsutural and peripheral bands; bands may blend into each other concealing background colour, ventral colour, outer and inner lip horn. Teleoconch rather smooth, with regular axial growth lines (Fig. 4E, Table 1).

Genital anatomy: Penial verge short (1/8–1/4 of penial chamber), broad, with pointed tip. Inner penial wall entirely covered with small pustules, arranged in rows over entire length of wall; three pilasters formed by rows of thickened, partly fused pustules (Fig. 11).

Comparative Remarks

Shell more conical and whorls more flattened in diameter than in species treated before. Dark brown colour of most shells with pronounced different ventral colour is also characteristic. Penial interior with three longitudinal pilasters formed by enlarged wall pustules is typical for this species only. For comparison with other species, see Solem (1981a: 198–199).

Distribution (Fig. 3)

Katers Island.

Amplirhagada decora Köhler, 2010
Figs. 4F, 12

Amplirhagada decora Köhler, 2010a: 240–242, figs. 33–35.

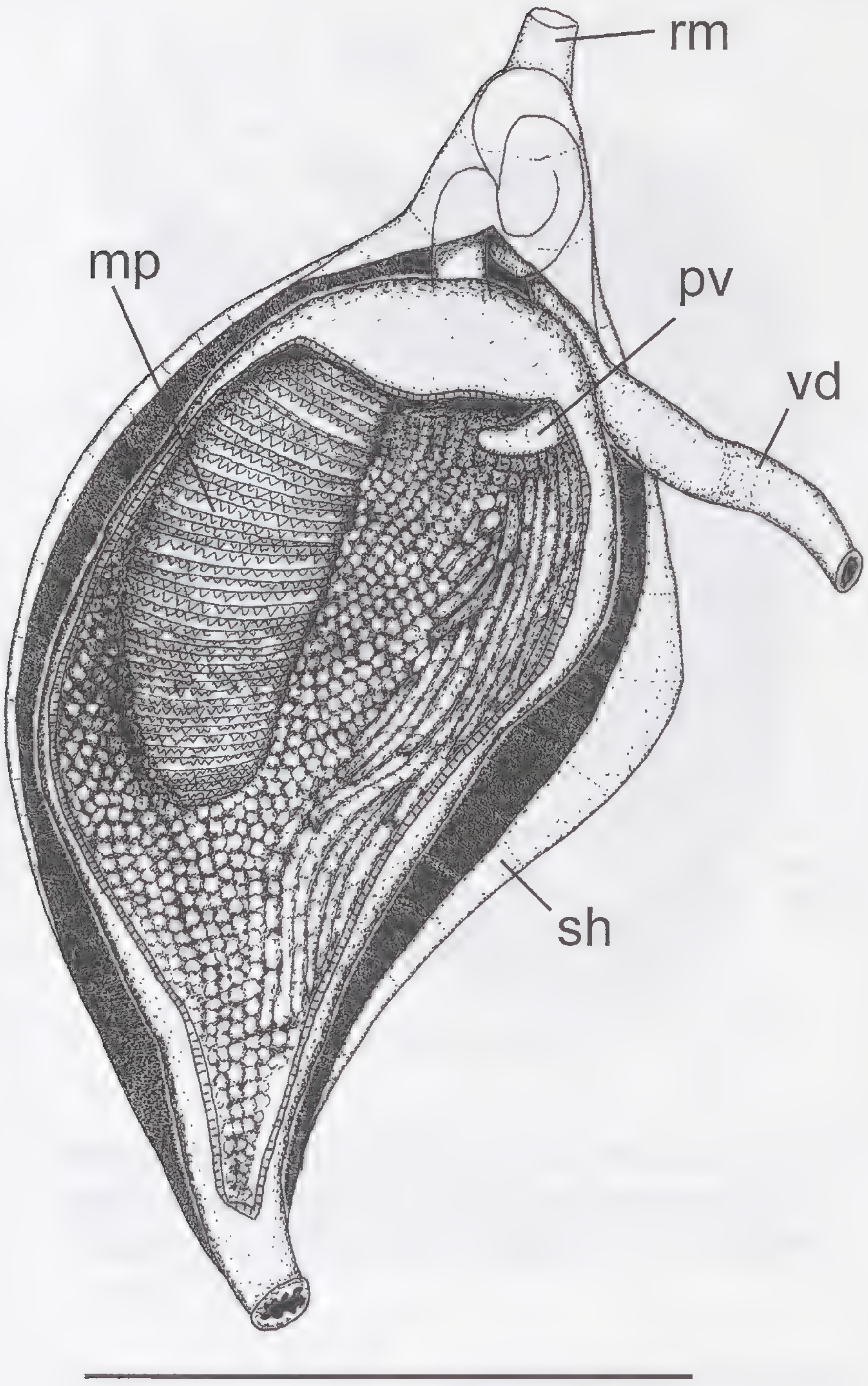

FIG. 12. Penial anatomy of *Amplirhagada decora* (AM C463698, Bigge Island; February). Scale bar = 5 mm.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Bigge Island, 4.3 km N of Savage Hill, 14°35'15"S, 125°11'05"E.

Material Examined

Holotype WAM S34609 (Fig. 4F). Paratypes AM C463698 (8 preserved specimens), WAM S36873 (17 preserved specimens) from type locality; AM C463699 (4 preserved specimens), WAM S36874 (9 preserved specimens) from 14°35'13.3"S, 125°11'10.5"E); AM C463700 (shell), WAM S36963 (2 shells) from 14°35'15"S, 125°11'05"E. Additional, non-type material WAM S36461–7, WAM S36652–4, WAM S36872 from Bigge Island.

Diagnosis

Shell: Broadly conical to subglobose, with medium to high spire; periphery angulated; upper sector of whorls flattened to rounded; umbilicus completely concealed; brownish horn with well-defined, dark brown, moderately broad subsutural and peripheral bands, most conspicuous on last whorls. Teleoconch sculptured with fine axial lirae, rounded in cross-section, evenly across shell surface, reduced underneath suture (Fig. 4F, Table 1).

Genital anatomy: Penial verge tiny. Inner penial wall with pustules of average size, densely arranged in rows over entire length of inner penial wall, partly fused to small elongated ridges; main stimulatory pilaster well-differentiated, forming a very large cone sculptured by dense ridges comprising apical to median portion of penial chamber; pilaster ridges with tiny hooks (Fig. 12).

Comparative Remarks

Dome-shaped shell as found only in some species, amongst which *A. decora* is one of the smallest and tallest (H/D larger than in most species). Conspicuous spiral banding is also typical; only *A. berthierana* Köhler, 2010, has a similarly shaped and coloured shell being on average larger in diameter. Rather large pustules of inner penial wall in combination with large, cone-shaped main pilaster with densely arranged hooks and tiny verge are diagnostic for *A. decora*; *A. berthierana* with smooth main stimulatory pilaster and larger verge.

Distribution (Fig. 3)

Bigge Island, in sympatry with *A. kessneri*.

Amplirhagada kessneri Köhler, 2010
Figs. 4G, 13

Amplirhagada kessneri Köhler, 2010a: 242–243, figs. 36–38.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Bigge Island, 4.3 km N of Savage Hill, 14°35'15"S, 125°11'05"E.

Material Examined

Holotype WAM S34610 (Fig. 4G). Paratypes AM C463701 (4 preserved specimens), WAM S36875 (10 preserved specimens) from type locality; AM C463702 (9 preserved specimens), WAM S36477 (5 shells), AM C463703 (2 shells), WAM S36658 (10 preserved specimens) from 14°35'16"S, 125°11'02"E; WAM S36876 (16 preserved specimens) from 14°35'18.5"S, 125°10'54.7"E.

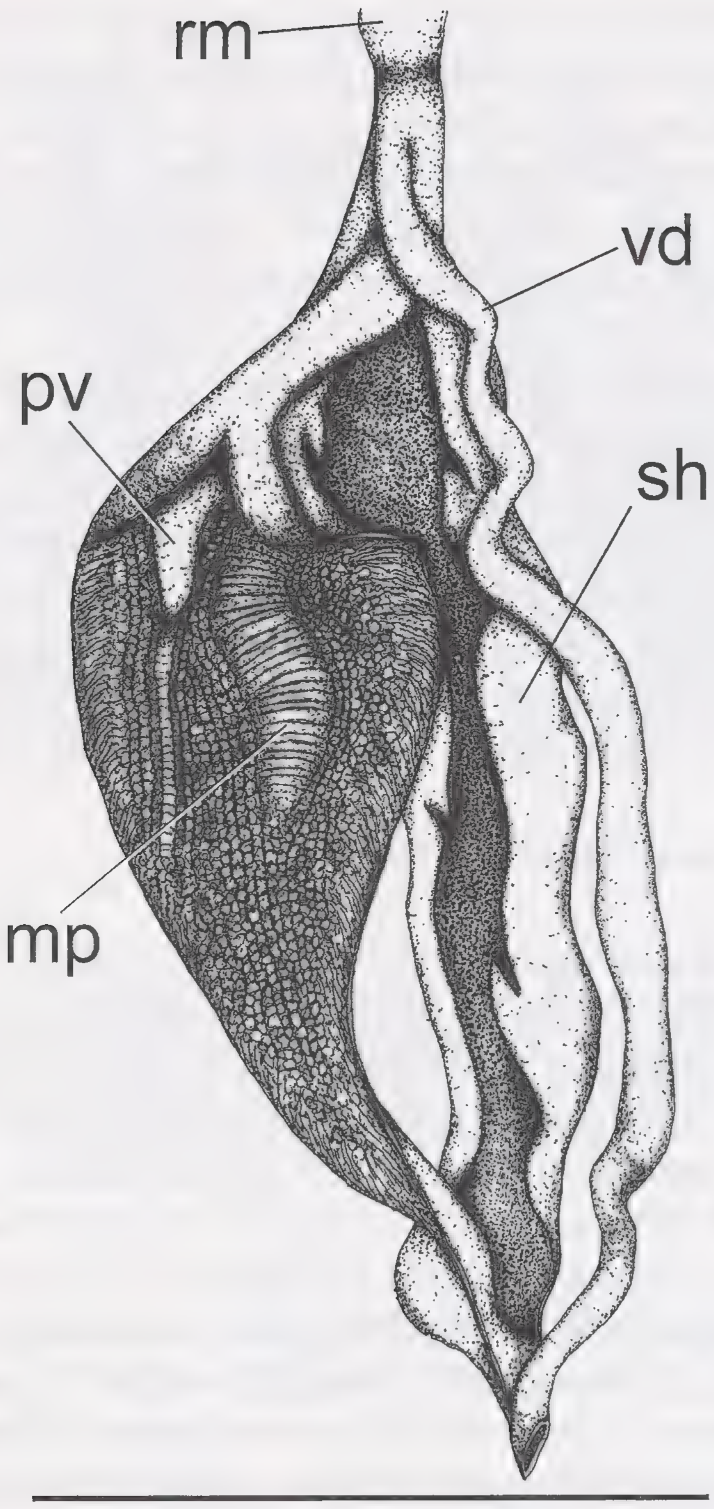

FIG. 13. Penial anatomy of *Amplirhagada kessneri* (WAM S36875, Bigge Island; February). Scale bar = 3 mm.

Diagnosis

Shell: Subglobose to conical with low spire; periphery evenly rounded to angulated; umbilicus forming a chink or open, 30–90% concealed; horn to light brown, exceptionally dark brown, brown subsutural and peripheral bands absent or diffuse to well marked, thin to moderately thick, most conspicuous on last whorls. Teleoconch sculptured with regularly spaced axial lirae becoming somewhat oblique on last whorl (Fig. 4G, Table 1).

Genital anatomy: Penial verge short (< 1/8 penial chamber), slender to spatulate, with truncated tip; penial wall pustules small, densely arranged in rows over entire length of inner penial wall; main stimulatory pilaster well differentiated, forming a large, elongated cone, sculptured by smooth horizontal ridges, on apical to median portion of penial chamber (Fig. 13).

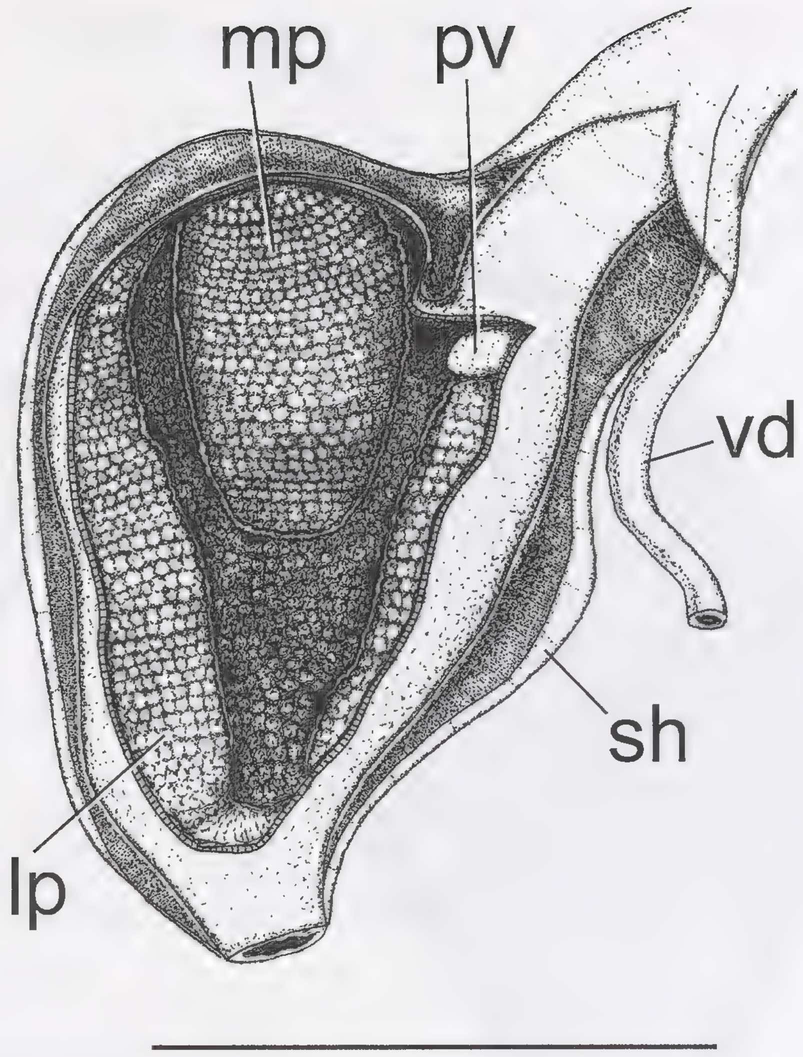

FIG. 14. Penial anatomy of *Amplirhagada boongareensis* (WAM S36655, Boongaree Island; August). Scale bar = 5 mm.

Comparative Remarks

Differs from most species by flatter, conspicuously angulated and uniformly reddish brown shell. From *A. decora* (also from Bigge Island), it also differs by a much smaller main pilaster and finer pustulation of inner penial wall.

Distribution (Fig. 3)

Bigge Island, in sympatry with *A. decora*.

Amplirhagada boongareensis Köhler, 2010
Figs. 4H, 14

Amplirhagada boongareensis Köhler, 2010a: 253–355, figs. 54–56.

Type Locality

Western Australia, Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04'36"S, 125°11'12"E.

Material Examined

Holotype WAM S34616 (Fig. 4H). Paratypes WAM S36655 (3 preserved specimens) from type locality; AM C463707 (8 shells), WAM S36455 (12 shells), WAM S36456 (15 shells)

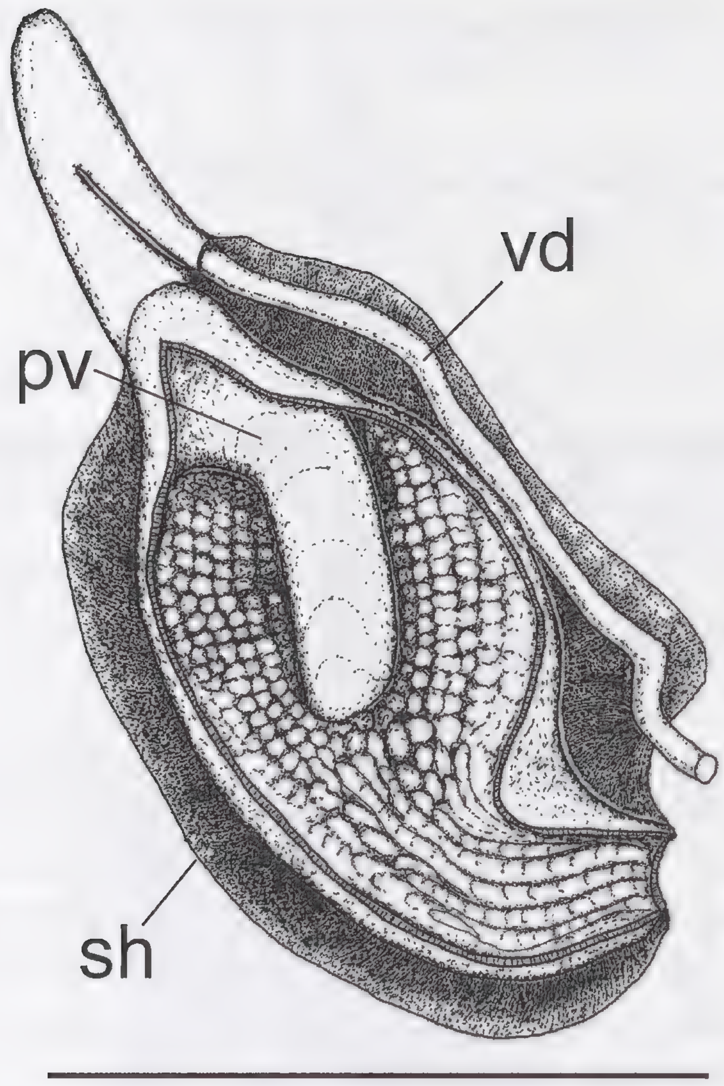

FIG. 15. Penial anatomy of *Amplirhagada gibsoni* (AM C463709, Boongaree Island; August). Scale bar = 5 mm.

from 15°04'31"S, 125°11'07"E; AM C463706 (6 shells), WAM S36458 (8 shells) from 15°04'16"S, 125°10'47"E); WAM S36656 (preserved specimens) from 15°04'09"S, 125°10'49"E.

Additional, non-type material WAM S36457, WAM S36459–60 from Boongaree Island.

Diagnosis

Shell: Beehive-shaped, with high spire; periphery slightly to clearly angulated; upper sector of whorls slightly shouldered, basal sector rounded; umbilicus 50–100% concealed; light brown, subsutural and peripheral bands may be absent or, if present diffuse to well marked, dark reddish brown, thin to moderately broad, most conspicuous on last whorl, bands may blend into each other covering entire surface of tip of shell with purplish brown colour; inner lip colour blends from reddish brown near parietal wall into horn at outer sections. Teleoconch with regular, fine axial lirae, rounded in cross-section, evenly distributed across shell surface, reduced in prominence underneath suture (Fig. 4H, Table 1).

Genital anatomy: Penial verge barely visible; penial wall pustules of average size, dense, randomly arranged across entire length of inner penial wall; main stimulatory pilaster well-differentiated, large, cone-shaped, covered by smooth, flattened pustules arranged in horizontal rows, comprising apical to median portion of penial chamber; two additional pilasters form along entire length of penial chamber covered by undifferentiated pustulation (Fig. 14).

Comparative Remarks

In proportion the tallest of all species (H/D < 1.12), *A. boongareensis* is characterized by its conspicuously high, beehive-shaped shell and its dark purplish-brown colour. Its heavily sculptured inner penial wall, which supports a very large main stimulatory pilaster, differs conspicuously from other species with dome-shaped shells, which frequently exhibit a smooth or simple penial wall sculpture without pustulation.

Distribution (Fig. 3)

Boongaree Island, in sympatry with *A. gibsoni*, *A. regia* and presumably another undescribed *Amplirhagada* species.

Amplirhagada gibsoni Köhler, 2010
Figs. 4I, 15

Amplirhagada gibsoni Köhler, 2010a: 255–256, figs. 57–59.

Type Locality

Western Australia, Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04'15"S, 125°11'14"E.

Material Examined

Holotype WAM S34617 (Fig. 4I). Paratypes AM C463709 (preserved specimen), WAM S36650 (2 preserved specimens) from type locality; AM C463708 (4 shells) from 15°04'15"S, 125°11'14"E; WAM S36468 (6 shells) from 15°04'36"S, 125°11'18"E; WAM S36469 (10 shells), WAM S36651 (preserved specimen) from 15°04'36"S, 125°11'18"E.

Diagnosis

Shell: Subglobose to conical with medium high spire; periphery evenly rounded to slightly angulated; upper and basal sectors of whorls rounded; umbilicus forming a chink or 90% concealed; uniformly light brownish to horn; inner lip white. Teleoconch sculptured with regular, fine axial lirae, rounded in cross-section, evenly distributed across shell surface, reduced underneath suture (Fig. 4I, Table 1).

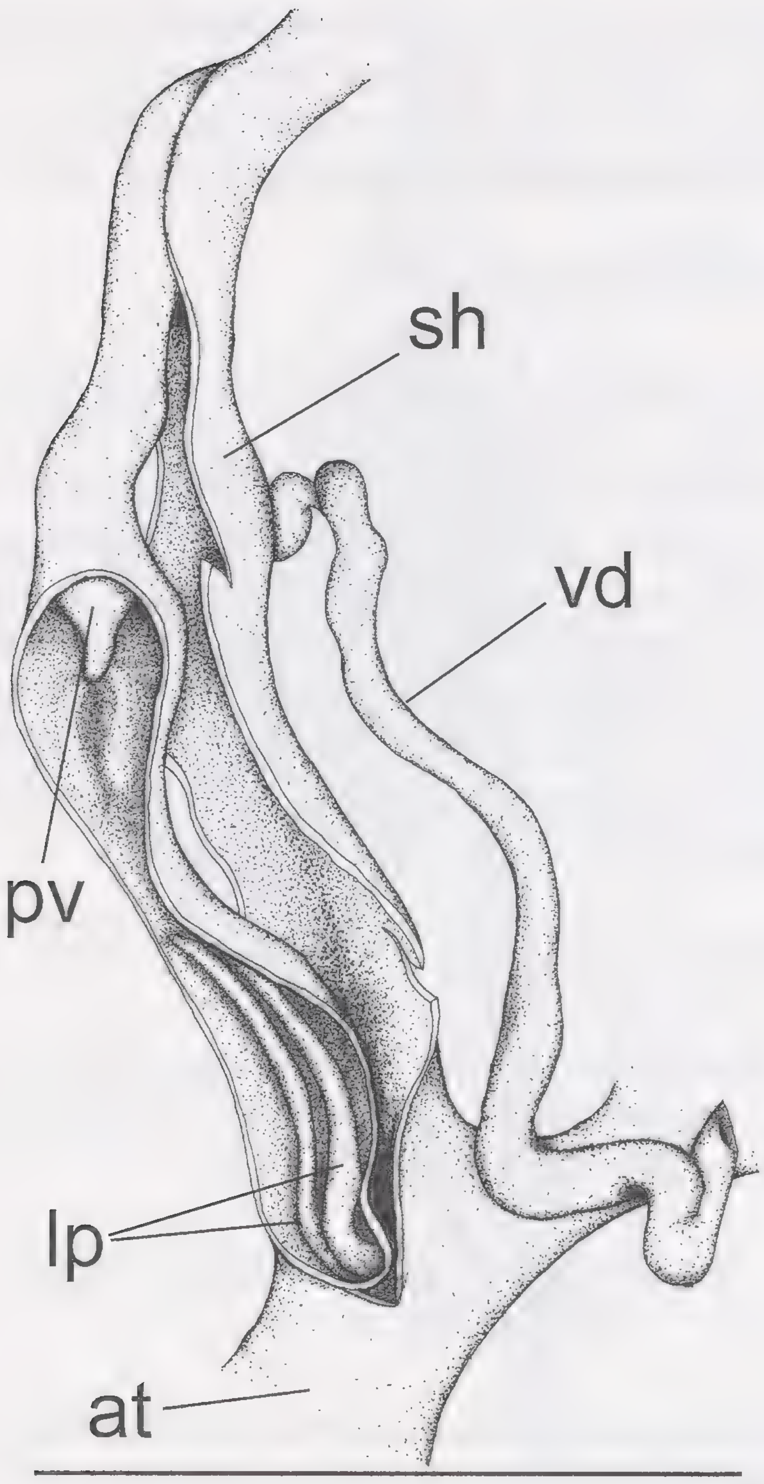

FIG. 16. Penial anatomy of *Amplirhagada regia* (WAM S36647, Boongaree Island; August). Scale bar = 5 mm.

Genital anatomy: Penial verge very long (ca. 1/3 penial chamber), broad, with pointed tip; penial wall pustules of normal size, randomly and densely arranged across entire length of inner penial wall, at base of penial chamber rows of fused pustules form 3–4 smooth longitudinal pilasters; main stimulatory pilaster absent (Fig. 15).

Comparative Remarks

Shell smaller in size, not as elevated in shape as in congeners from same island. Large pustules and very large penial verge are diagnostic.

Distribution (Fig. 3)

Boongaree Island, in sympatry with *A. boongareensis*, *A. regia* and presumably another undescribed *Amplirhagada* species.

Amplirhagada regia Köhler, 2010

Figs. 4J, 16

Amplirhagada regia Köhler, 2010a: 251–253, figs. 51–53.

Type Locality

Western Australia, Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04’15”S, 125°11’14”E.

Material Examined

Holotype WAM S34615 (Fig. 4J). Paratypes AM C463705 (4 preserved specimens), WAM S36647 (3 preserved specimens) from type locality; WAM S36449 (6 preserved specimens) from 15°04’00”S, 125°11’11”E; AM C463704 (6 shells), WAM S36480 (12 shells) from 15°04’31”S, 125°11’07”E.

Additional, non-type material WAM S36479, WAM S36481–5, WAM S36648 from Boongaree Island.

Diagnosis

Shell: Globose with medium high to high spire, solid to thick, periphery angulated, upper sector of whorls rather flattened, basal sector rounded, umbilicus 60–100% concealed; colour uniformly cremish horn, outer lip purple, inner lip pale purple. Teleoconch smooth, except faint axial growth lines (Fig. 4J, Table 1).

Genital anatomy: Penial verge short (< 1/8 penial chamber), slender to spatulate, with pointed tip; penial wall smooth, with two longitudinal pilasters at basal portion of penial chamber, plus two weakly developed pilasters at apical portion (Fig. 16).

Comparative Remarks

Diagnostic features are broadly conical to dome-shaped shell, smooth inner penial wall with lack of pustulation and main pilaster (penial wall sculpture differs conspicuously from sympatric congeners; see above).

Distribution (Fig. 3)

Boongaree Island, in sympatry with *A. boongareensis*, *A. gibsoni* and presumably another undescribed *Amplirhagada* species.

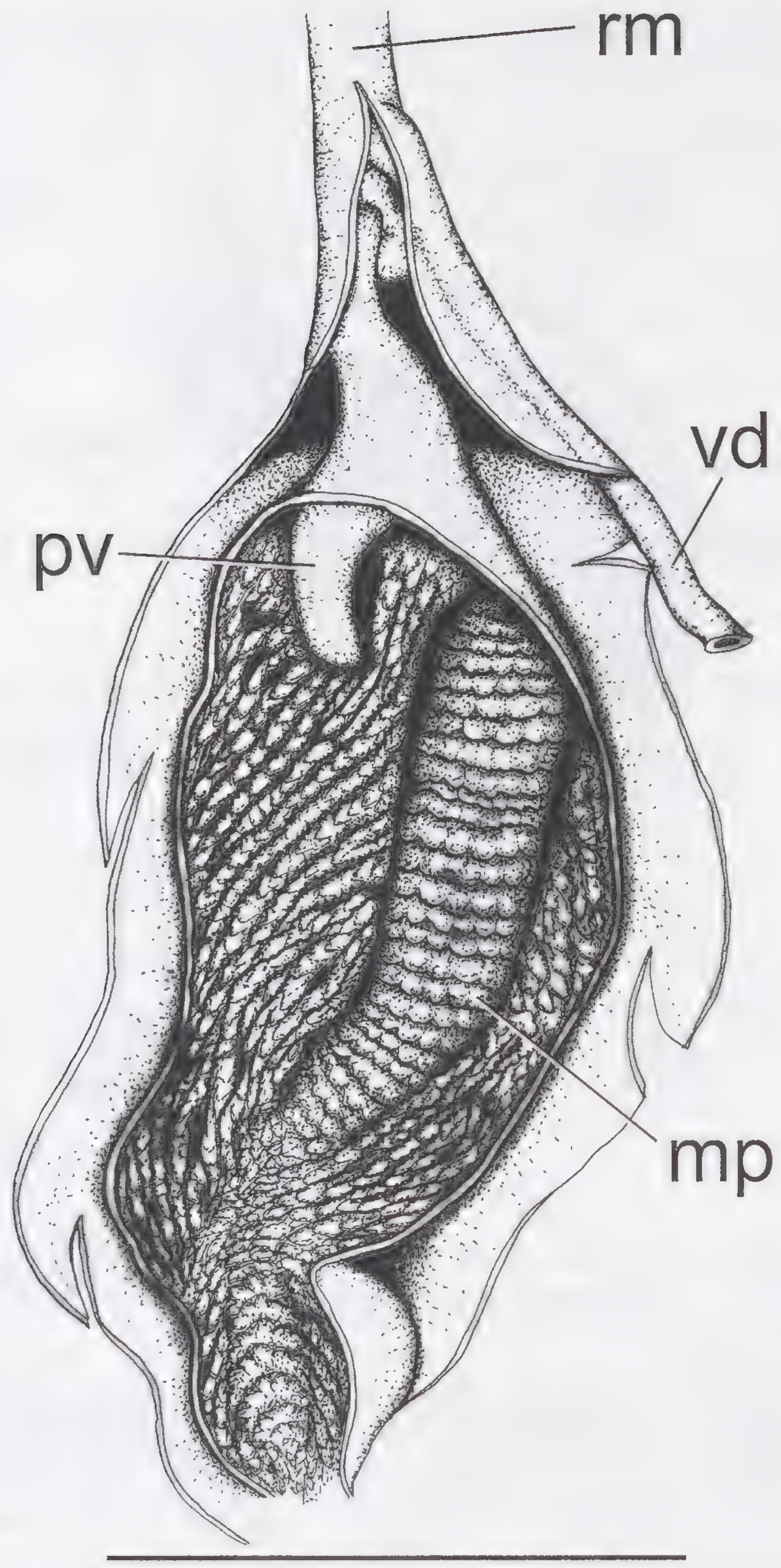

FIG. 17. Penial anatomy of *Amplirhagada yorkensis* (AM C463711, Coronation Island; May). Scale bar = 3 mm.

Amplirhagada yorkensis Köhler, 2010
Figs. 4L, 17

Amplirhagada yorkensis Köhler, 2010a: 257–259, figs. 61–63.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, York Sound, southern section of Coronation Island, 15°01'52"S, 124°56'56"E.

Material Examined

Holotype WAM S34619. Paratypes AM C463711 (24 preserved specimens), WAM S36979 (42 preserved specimens).

Additional, non-type material WAM S37376–8, WAM S36980–6, WAM S37394–404, AM C463712–4 (Coronation Island, southern and northern sections).

Diagnosis

Shell: Broadly conical with low spire, periphery evenly rounded to slightly angulated, upper and basal sectors of whorls rounded, umbilicus open, 30–90% concealed; brownish horn, subsutural band absent, peripheral band absent or diffuse, light yellowish brown, thin, only visible on last whorl(s). Teleoconch smooth except axial growth lines (Fig. 4L, Table 1).

Genital anatomy: Penial verge very short; penial wall pustules of average size, arranged in rows across entire length of inner penial wall; main stimulatory pilaster well-differentiated, large, cone-shaped, sculptured by horizontal ridges that support little hooks, comprising about 3/4 of length of penial chamber (Fig. 17).

Comparative Remarks

Typical for this species is comparatively small, low-spired shell, well-rounded periphery and pale colour; penis with a comparatively large main pilaster.

Distribution (Fig. 3)

Coronation Island. Potentially also on adjacent islands and islets and the adjacent mainland.

Amplirhagada uwinsensis Köhler, 2010
Figs. 4M, 18–19

Amplirhagada uwinsensis Köhler, 2010a: 261–263, figs. 67–69.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Hanover Bay, Uwins Island, 15°15'32"S, 124°46'08"E.

Material Examined

Holotype WAM S34621. Paratypes AM C463715 (15 preserved specimens), WAM S36991 (35 preserved specimens) from type locality; AM C463716 (15 shells), WAM S37441 (30 shells) from 15°15'25"S, 124°48'04"E.

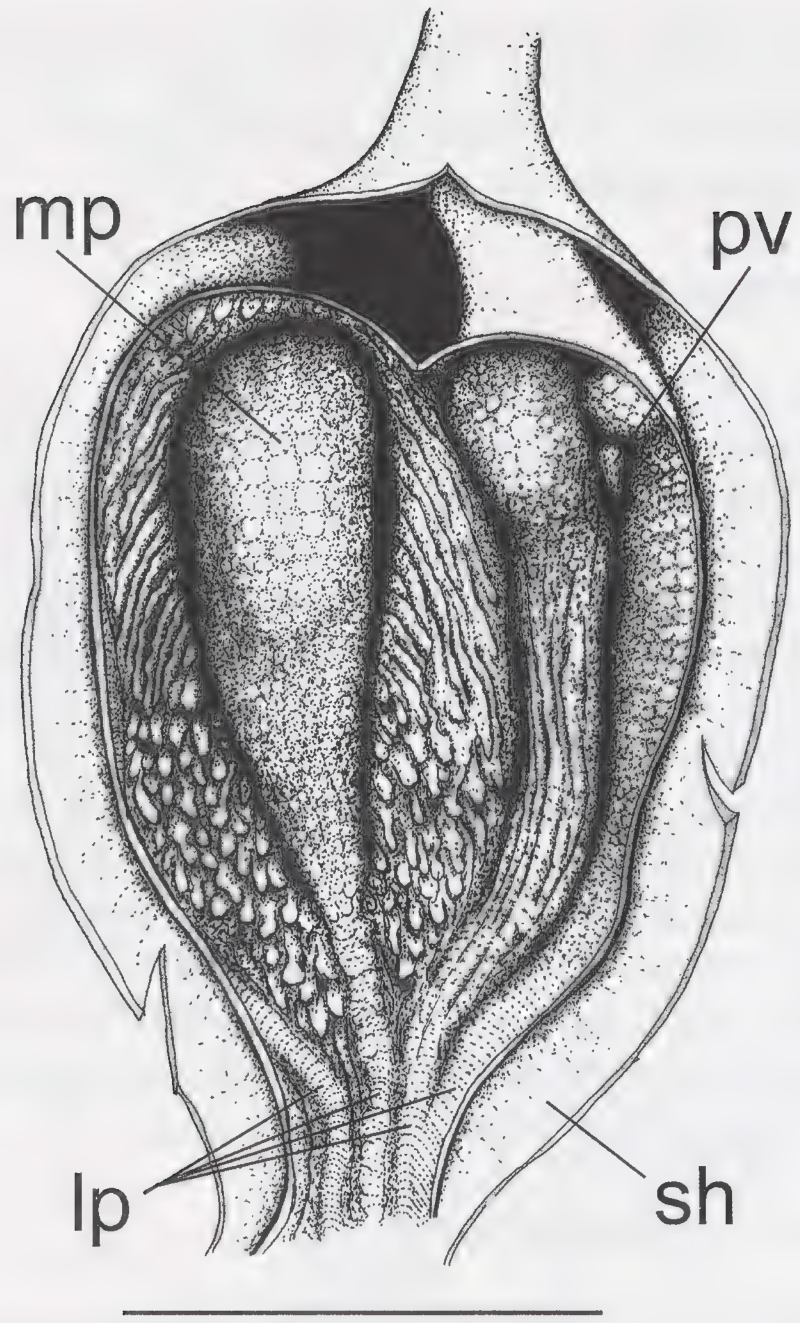

FIG. 18. Penial anatomy of *Amplirhagada uwinsensis* (AM C463715, Uwins Island; August). Scale bar = 5 mm.

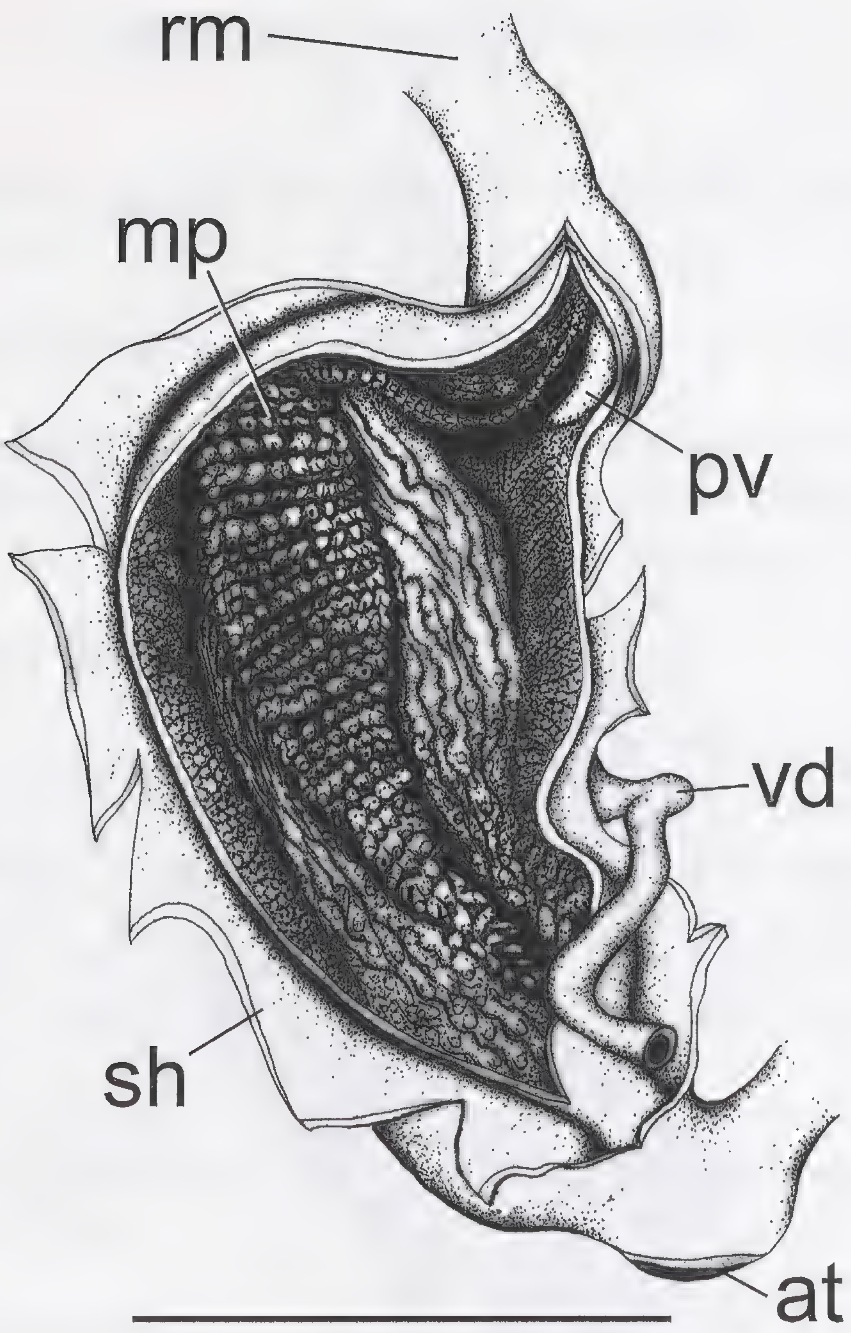

FIG. 19. Penial anatomy of *Amplirhagada uwinsensis* (FMNH 2219102, Myctiys Island; August). Scale bar = 5 mm.

Additional, non-type material AM C463717, WAM S36987–90, WAM S37440, WAM S37442–4, from Uwins Island; AM C471712 (20 preserved specimens), WAM S37664 (51 preserved specimens) from Mictyis Island, 2.5 km NW of Uwins Island; 15°13'12"S, 124°47'23"E; FMNH 219102 from Mictyis Island, 15°13'05"S, 124°47'20"E.

Diagnosis

Shell: Subglobose, beehive-shaped, with medium high spire; periphery angulated; upper and basal sectors of whorls rounded; umbilicus completely concealed; light reddish brown with light to chestnut brown, diffuse to well-defined subsutural and peripheral band, bands may blend into each other covering entire surface, outer lip blending into chestnut brown, inner lip blending into dark ochre to chestnut brown. Teleoconch with marked radial growth lines becoming oblique towards base of shell (Fig. 4M, Table 1).

Genital anatomy: Penial verge barely visible; penial wall pustules comparatively large, elongated, arranged in rows on median and basal portion of penial chamber, forming densely packed, narrow longitudinal pilasters at apical end of penial chamber; main stimulatory pilaster well-differentiated, large, cone-shaped, covered with flattened pustules, comprising distal to median portion of penial chamber; two additional pilasters form along wall, covered by flattened pustules or smooth narrow ridges (Figs. 18, 19).

Comparative Remarks

One of the species with large, dome-shaped shells; conspicuously differing from *A. tricenaria* Köhler, 2010, and *A. regia* by dark brown outer lip colour and huge, cone-shaped main pilaster, presence of additional pilasters and characteristically elongated pustules of inner penial wall. Material from Mictyis Island kept in FMNH was identified by Solem as "*Amplirhagada* NSP 66" exhibits identical genital anatomy (only differing by presence of little hooks on main pilaster) (Fig. 19), and is considered as conspecific. A sample of immature specimens from adjacent mainland (WAM S37669, 1.3 km S of Halfway Bay, 15°20'15"S, 124°49'23"E) is differentiated by 3% uncorrected genetic p-distance in 16S; for immature state of specimens, species identity remains questionable.

Distribution (Fig. 3)

Uwins and Mictyis islands.

Amplirhagada sphaeroidea Köhler, 2010
Figs. 4N, 20

Amplirhagada sphaeroidea Köhler, 2010a: 263–264, figs. 70–72.

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, St. Andrews Island, 15°21'24"S, 124°59'46"E.

Material Examined

Holotype WAM S34622 (Fig. 4N). Paratypes AM C463718 (2 preserved specimens), WAM S37029 (7 preserved specimens) from type locality; AM C463719 (shell), WAM S37027 (3 preserved specimens), WAM S37411 (shell) from 15°21'34"S, 125°00'07"E). Additional, non-type material WAM S37028, WAM S37030, WAM S37410–12, WAM S49000–1 from St. Andrews Island.

Diagnosis

Shell: Globose to subglobose, beehive-shaped, with medium high spire; solid to thick; periphery angulated; upper sector of whorls rather flattened, basal sector rounded; umbilicus 90–100% concealed; colour blends from horn at base to lightly brownish at top of shell, subsutural and peripheral bands absent or diffuse, brownish, visible on last whorl(s) only; ventrally crème; outer lip dark brownish-purple; inner lip blending from dark pink outside to horn deeper inside. Teleoconch smooth except faint growth lines (Fig. 4N, Table 1).

Genital anatomy: Penial verge short (< 1/8 penial chamber), slender with pointed tip; penial wall pustules fused, forming regular, smooth, diagonal, delicate lamellae on apical portion, becoming more and more oblique towards anterior end of penial chamber; main stimulatory pilaster elongated, large, cone-shaped, corrugated, comprising apical portion of penial chamber and gradually decreasing in size anteriorly; three additional, smooth, narrow, rather indistinct pilasters form at anterior base of penial chamber (Fig. 20). Vas deferens entering penial sheath apically.

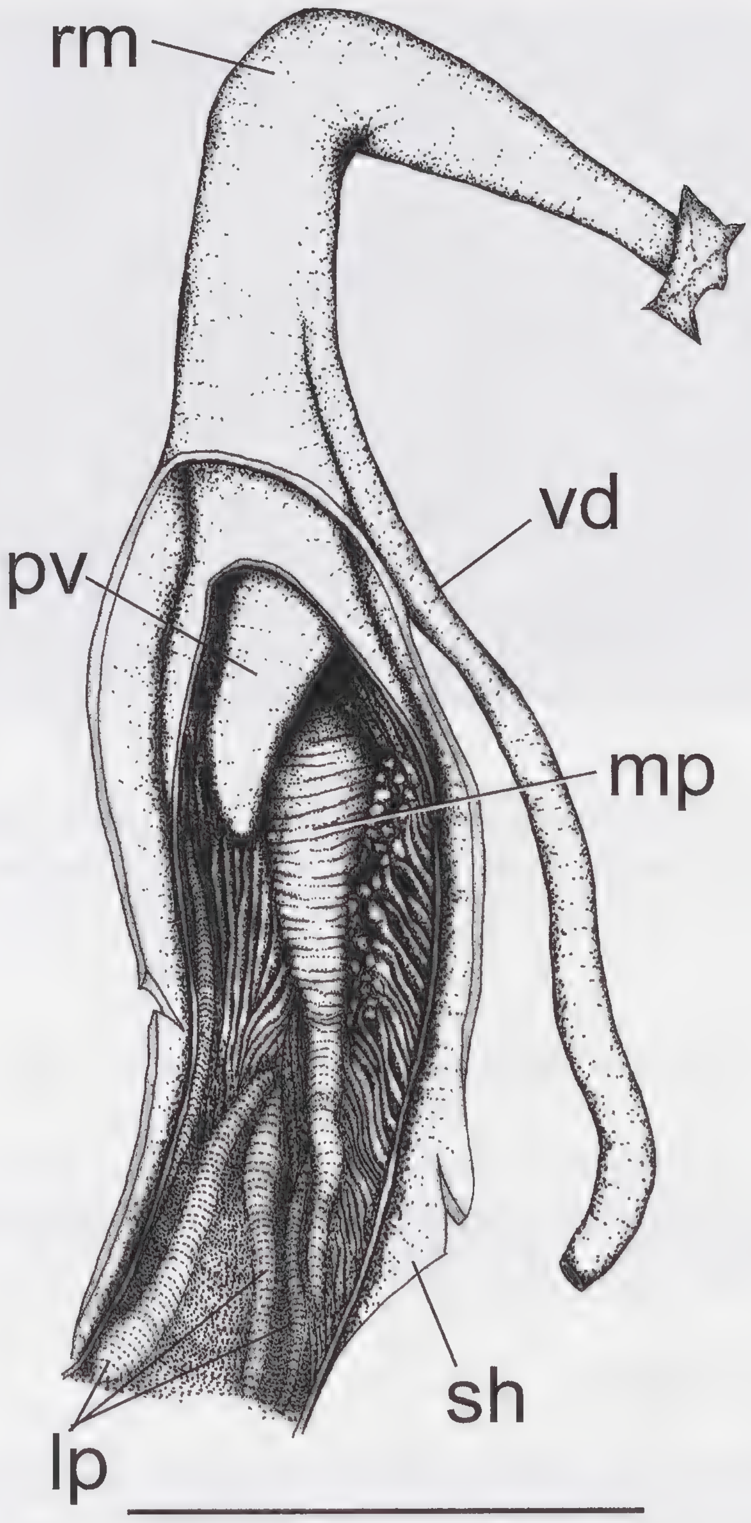

FIG. 20. Penial anatomy of *Amplirhagada sphaeroidea* (WAM S37027, St. Andrews Island; May). Scale bar = 3 mm.

Comparative Remarks

One of the few species with large, dome-shaped shells; differing from *A. tricenaria* and *A. regia* by dark outer lip and from *A. uwinsensis* by purplish colour of outer lip. Covering of inner penial wall with lamellae, elongate-conical, corrugated main pilaster, and relatively large verge are diagnostic.

Distribution (Fig. 3)

St. Andrews Island, in sympatry with *A.* cf. *pusilla* Solem, 1981.

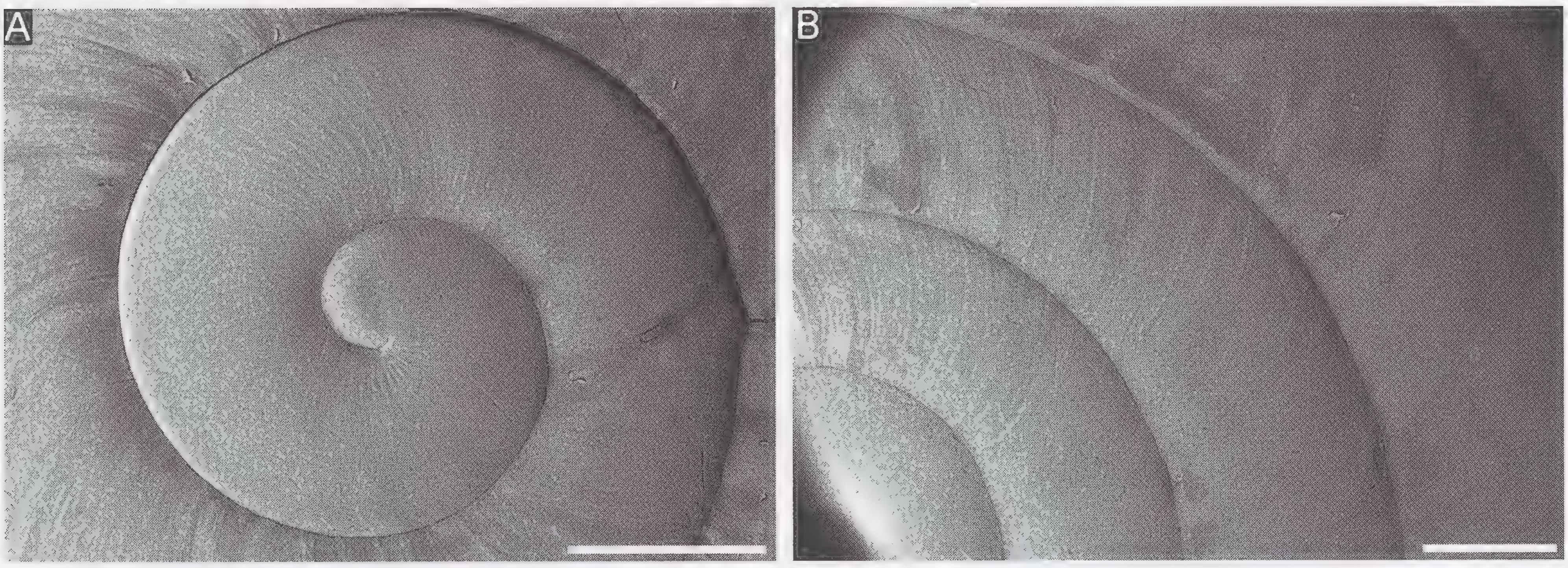

FIG. 21. SEM micrographs of the shell of ***Amplirhagada globosa*** n. sp. paratype AM C471713 (St. Patrick Island). A: Apical view showing protoconch; B: Sculpture on first four whorls viewed from above. Scale bars = 1 mm.

Amplirhagada cf. *pusilla* Solem, 1981
Fig. 4O

Amplirhagada pusilla Solem, 1981a: 194–198, pl. 12c, figs. 37c, 38e, f, 41b, 42.

Type Locality

Western Australia, northwestern Kimberley, Prince Regent Reserve, Pitta Creek Gorge.

Material Examined

WAM S37405–9 (shells) from St. Andrew Island, 15°21’26–36”S, 124°59’41–52”E.

Diagnosis

Shell: Comparatively small, broadly conical with rather low spire and sharply angulated periphery; last whorl weakly descending before aperture; umbilicus open, 0–50% concealed; background colour pale (whitish) with well-developed, narrow, slightly diffuse brown spiral band slightly above periphery; subsutural band inconspicuous. Teleoconch sculptured by radial growth lines, surface somewhat glossy; aperture simple rounded, apertural lip slightly thickened, expanded, slightly reflected; basal node weakly developed (Fig. 4O, Table 1).

Comparative Remarks

Only dry shells available, which correspond well with Solem’s (1981a) description of *A. pusilla*. This species is characterised by rather small, flat shell (H/D ~ 0.59) with open umbilicus. However, shells alone do not permit unequivocal identification of species deeming the current determination provisional. *Amplirhagada yorkensis* is similar in shell size and shape but has a wider umbilicus, not as well-developed spiral bands.

Distribution (Fig. 3)

Upper Prince Regent Reserve; possibly including St. Andrews Island.

Amplirhagada globosa n. sp.
Figs. 4P, 21–23

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, St. Patrick Island; 15°21’23”S, 124°57’55”E; coll. Vince Kessner, 9/02/2009, KIS 2–64 (Vine thicket on steep slopes, sandstone boulders. Resting on trees and boulders).

Material Examined

Holotype WAM S58432 (preserved specimen; Fig. 4P). Paratypes WAM S37665 (25 preserved specimens), AM C471713 (10 preserved specimens), AM C471714 (6 shells) WAM S37999 (10 shells), from type locality.

Etymology

From “*globosa*” (Latin = round, spherical, globular) referring to its globose shell; adjective of feminine gender.

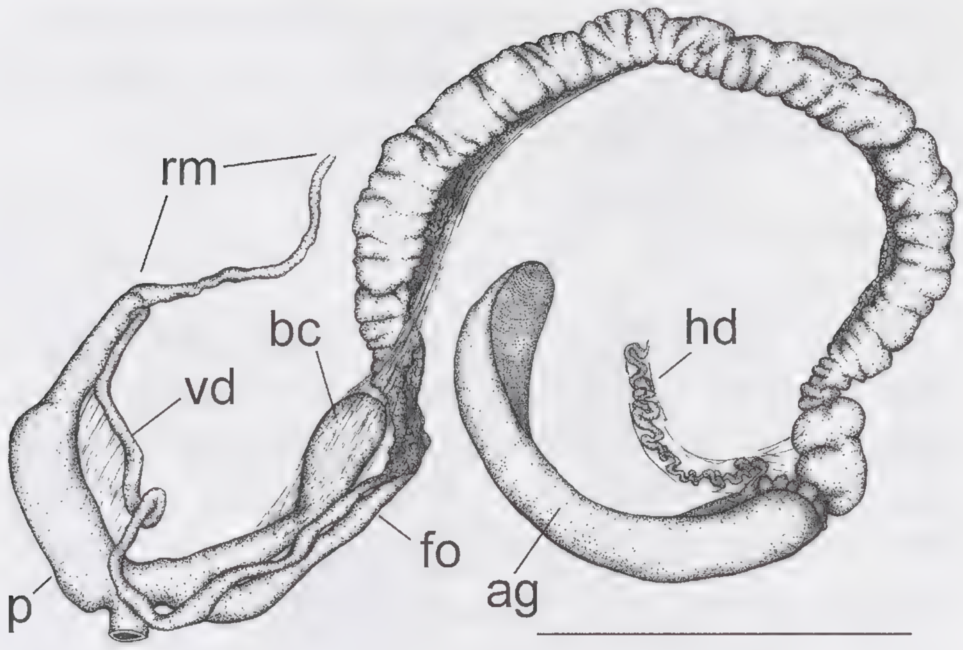

FIG. 22. Genital anatomy of ***Amplirhagada globosa*** n. sp. paratype AM C471713 (St Patrick Island; February). Scale bar = 10 mm.

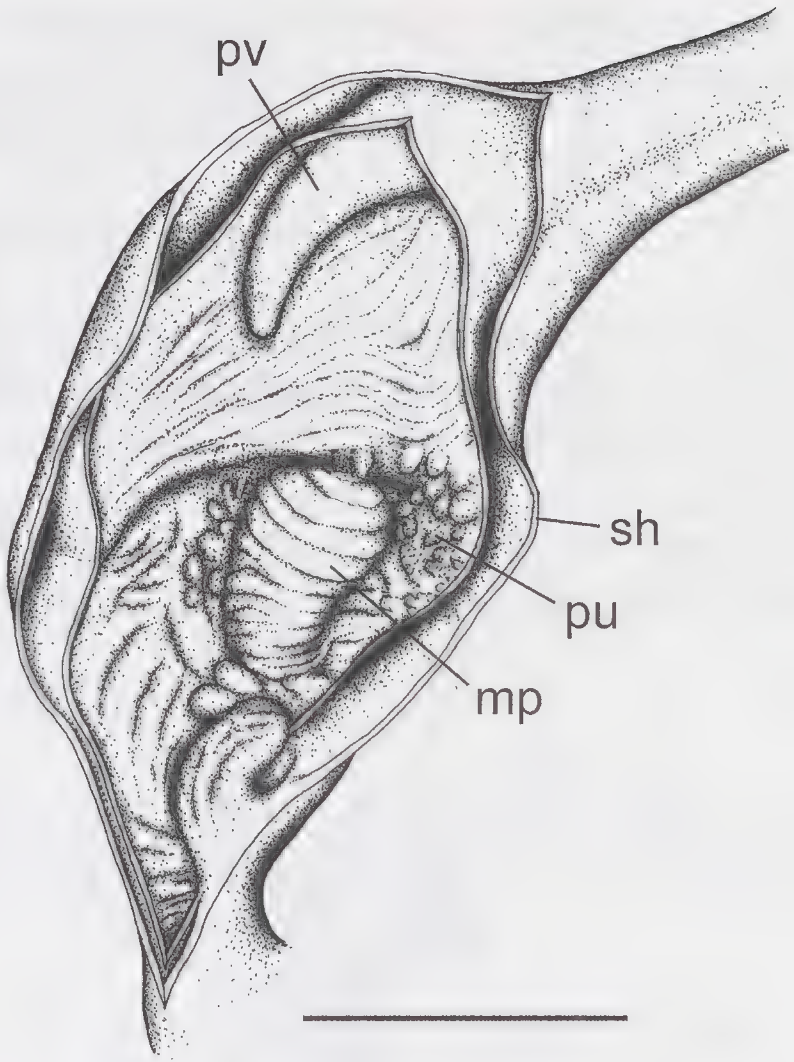

FIG. 23. Penial anatomy of ***Amplirhagada globosa*** n. sp. paratype AM C471713 (St Patrick Island; February). Scale bar = 2 mm.

Description

Shell (Figs. 4P, 21; Table 1): Globose to subglobose, beehive shaped, with medium high spire, solid to thick; periphery markedly angulated, upper sector of whorls rather flat, basal sector rounded; umbilicus open, 70–90% concealed; lightly brown, subsutural and peripheral bands absent or diffuse, thin, brown, visible on last whorl(s) only, outer lip dark chestnut brown, inner lip blending from dark brownish pink outside to horn deeper inside. Protoconch 2.8 mm in diameter, comprising about 1.2 whorls, rather smooth. Teleoconch smooth except faint growth lines. Angle of aperture 45°; outer lip rounded, thick, slightly to well expanded, slightly reflected, basal node of lip weak, palatal node absent.

Genital anatomy (Figs. 22–23): Penis about as long as anterior part of oviduct, straight, bulbous penis proper restricted to proximal 2/3 of penial complex; vas deferens forming simple loop before entering penis; penial retractor muscle equivalent to about 2/3 of penial length; penial sheath thick; verge large (~ 1/4 penial chamber), elongate; penial wall densely covered with minute pustules, predominantly smooth, a few, irregularly arranged pustules forming at mid-portion; main stimulatory pilaster broadly cone-shaped, consisting of broad lateral ridges, comprising central portion of penial chamber. Vas deferens entering penial sheath apically, reflexing within sheath before entering penis proper. Vagina short, distally inflated, inner vaginal wall densely covered with minute pustules, predominantly smooth with few, indistinct longitudinal pilasters. Bursa copulatrix moderately wide; with inflated head, connected with oviduct by connective tissue.

Comparative Remarks

Anatomical description based on dissection of three specimens. Most similar with *A. sphaeroidea* from St. Andrews Island, *A. camdenensis* from Augustus Island and *A. uwinsensis* from Uwins Island. Differing from *A. sphaeroidea* by proportionally higher shell (smaller diameter, same height), from *A. camdenensis* by proportionally higher shell (same diameter, lower height). Most distinct sculpture of inner penial wall with ***A. globosa*** lacking obliquely lateral lamellae and main pilaster tapering anteriorly as in *A. sphaeroidea* but having a well-differentiated main stimulatory pilaster, which is lacking in *A. camdenensis*. *Amplirhagada uwinsensis* has a similar shell, but more vividly coloured, purplish-brown aperture and completely concealed umbilicus; also differing from ***A. globosa*** by very strongly sculptured inner penial wall with huge main stimulatory pilaster and two accessory pilasters.

Distribution (Fig. 3)

St. Patrick Island.

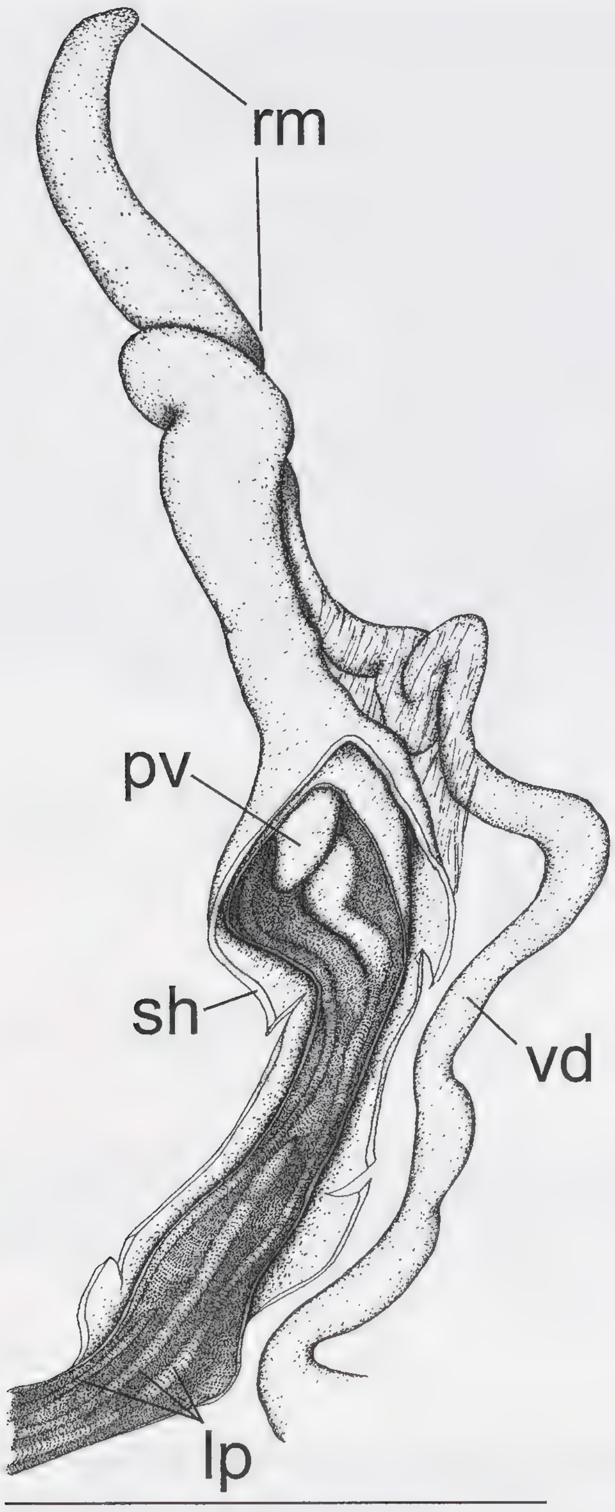

FIG. 24. Penial anatomy of *Amplirhagada basilica* (paratype AM C463720, Augustus Island; June). Scale bar = 3 mm.

Amplirhagada basilica Köhler, 2010
Figs. 4Q, 24

Amplirhagada basilica Köhler, 2010a: 264–266, figs. 73–75.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Brecknock Harbour, southern section of Augustus Island, 15°23’53”S, 124°036’03”E.

Material Examined

Holotype WAM S34623 (Fig. 4Q). Paratypes AM C463720 (4 preserved specimens), WAM S37004 (11 preserved specimens) from type locality; AM C463721 (3 shells), WAM S37414 (4 shells) from 15°22’54”S, 124°35’24”E. Additional, non-type material WAM S37000–3, WAM S37413, WAM S49002, WAM S49004 from southern section of Augustus Island.

Diagnosis

Shell: Subglobose, broadly beehive shaped, with medium high spire, periphery slightly angulated, upper and basal sectors of whorls rounded, umbilicus 80–95% concealed; colour blending from crème into brownish (upper sector of lower whorls darker), subsutural band diffuse, light brownish, peripheral band diffuse, brownish, visible on last whorls only, outer lip brownish purple, inner lip pinkish. Teleoconch smooth except indistinct growth lines (Fig. 4Q, Table 1).

Genital anatomy: Penial verge comprising 1/8–1/4 of penial chamber; penial wall smooth, main stimulatory pilaster absent, two smooth, narrow longitudinal pilasters form along entire length of penial chamber, two additional smooth, narrow pilasters form at anterior base (Fig. 24). Vas deferens entering penial sheath apically.

Comparative Remarks

One of the species with dome- to beehive-shaped shells; being among the largest species of the genus; differing from *A. tricenaria* and *A. regia* by dark outer lip. Purplish colour of outer lip similar to *A. sphaeroidea*. Absence of penial wall pustules is diagnostic.

Distribution (Fig. 3)

Augustus Island, in sympatry with *A. camdenensis* Köhler, 2010, in the northwestern part of the island.

Amplirhagada camdenensis Köhler, 2010
Figs. 4R, 25

Amplirhagada camdenensis Köhler, 2010a: 266–268, figs. 76–78.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, northwestern section of Augustus Island, 15°20’16”S, 124°31’16”E.

Material Examined

Holotype WAM S34624 (Fig. 4R). AM C463722 (3 preserved specimens), WAM

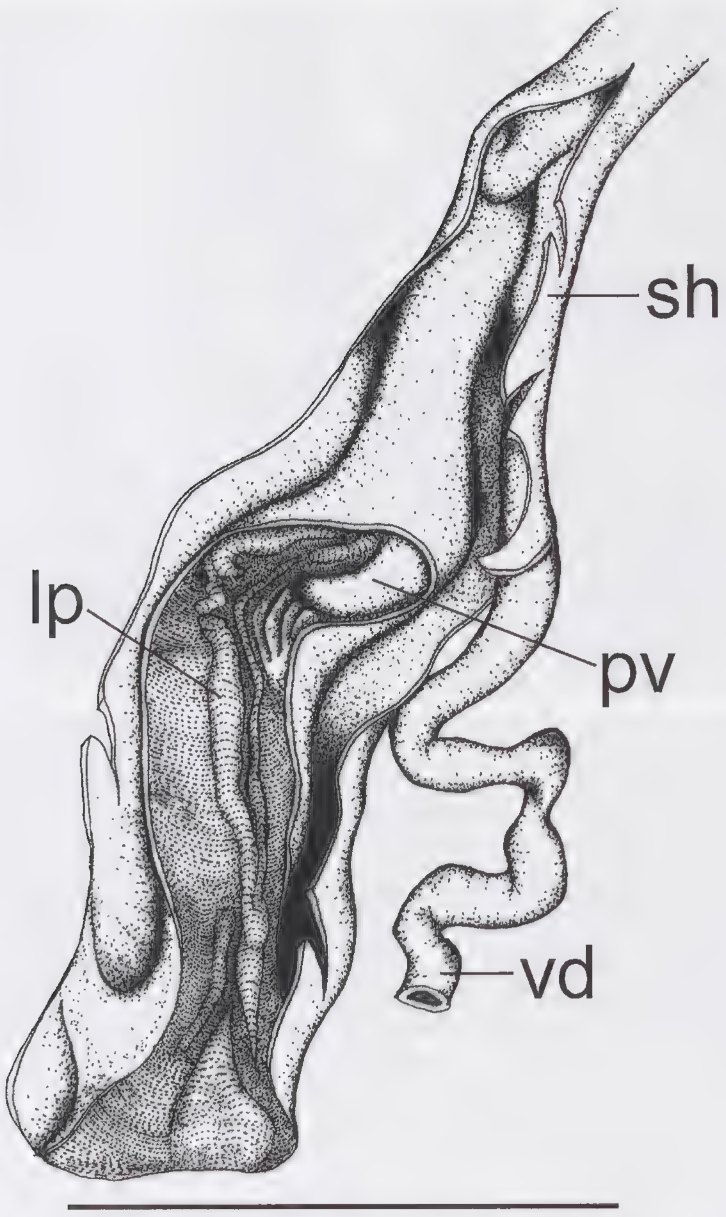

FIG. 25. Penial anatomy of *Amplirhagada camdenensis* (paratype AM C463722, Augustus Island; May). Scale bar = 3 mm.

S37006 (5 preserved specimens) from type locality; WAM S37005 (3 preserved specimens) from 15°20'59"S, 124°31'30"E. Additional, non-type material WAM S37007–8, WAM S37445–50, WAM S41481, FMNH 219063 from NW Augustus Island.

Diagnosis

Shell: Globose, with medium to high spire, solid, periphery evenly rounded to slightly angulated, upper sector of whorl flattened to slightly shouldered, basal sector rounded, umbilicus 40–100% concealed; yellowish brown to horn, subsutural and peripheral bands diffuse, dark to chestnut brown, becoming more indistinct or blurring towards tip of whorl, bands may blend into each other covering shell in light brown colour, whitish creme to yellowish brown ventrally, outer and inner lip colour pinkish brown. Teleoconch smooth except faint axial growth lines (Fig. 4R, Table 1).

Genital anatomy: Penial verge rather short (1/8–1/4 of length of penial chamber), broad; inner penial wall smooth; main stimulatory pilaster inconspicuous, narrow, smooth, on apical to median portion of penial chamber; one to three additional, smooth, narrow pilasters form distally (Fig. 25).

Comparative Remarks

Identified by Solem as "*Amplirhagada* sp. 65"; smallest of all species with dome- to beehive-shaped shell, with significantly larger H/D ratio than most other species (Table 1). Absence of penial wall pustules and smooth, longitudinal pilasters of inner penial wall are diagnostic.

Distribution (Fig. 3)

Northwestern part of Augustus Island, in sympatry with *A. basilica*; not found in the southern part of the island.

Amplirhagada sinenomine n. sp.

Figs. 4S–T, 26–28

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, unnamed island in Doubtful Bay; 15°54'52.7"S, 124°27'47.8"E; coll. Vince Kessner, 26/05/2009, KIS 3–155 (dense patches of vine thicket at the base of sandstone outcrops; under piles of rocks).

Material Examined

Holotype WAM S37710 (preserved specimen, dissected). Paratypes WAM S37709 (4 preserved specimens), WAM S58433 (2 preserved specimens), WAM S58434 (2 preserved specimens); WAM S37711 (shell); AM C471715 (3 shells), AM C471716 (3 shells), WAM S37802 (5 shells), WAM S37803 (2 shells), WAM S37804 (2 shells), WAM S37805 (7 shells), WAM S37806 (5 shells), WAM S37807 (7 shells) from unnamed Island in Doubtful Bay.

Etymology

From "*sine nomine*" (Latin = without a name) referring to the type locality, an unnamed island in Doubtful Bay; noun in apposition.

Description

Shell (Figs. 4S–T, 26A–D; Table 1): Broadly conical to subglobose with rather high spire; periphery well rounded to slightly depressed, upper and basal sector of whorls convex; um-

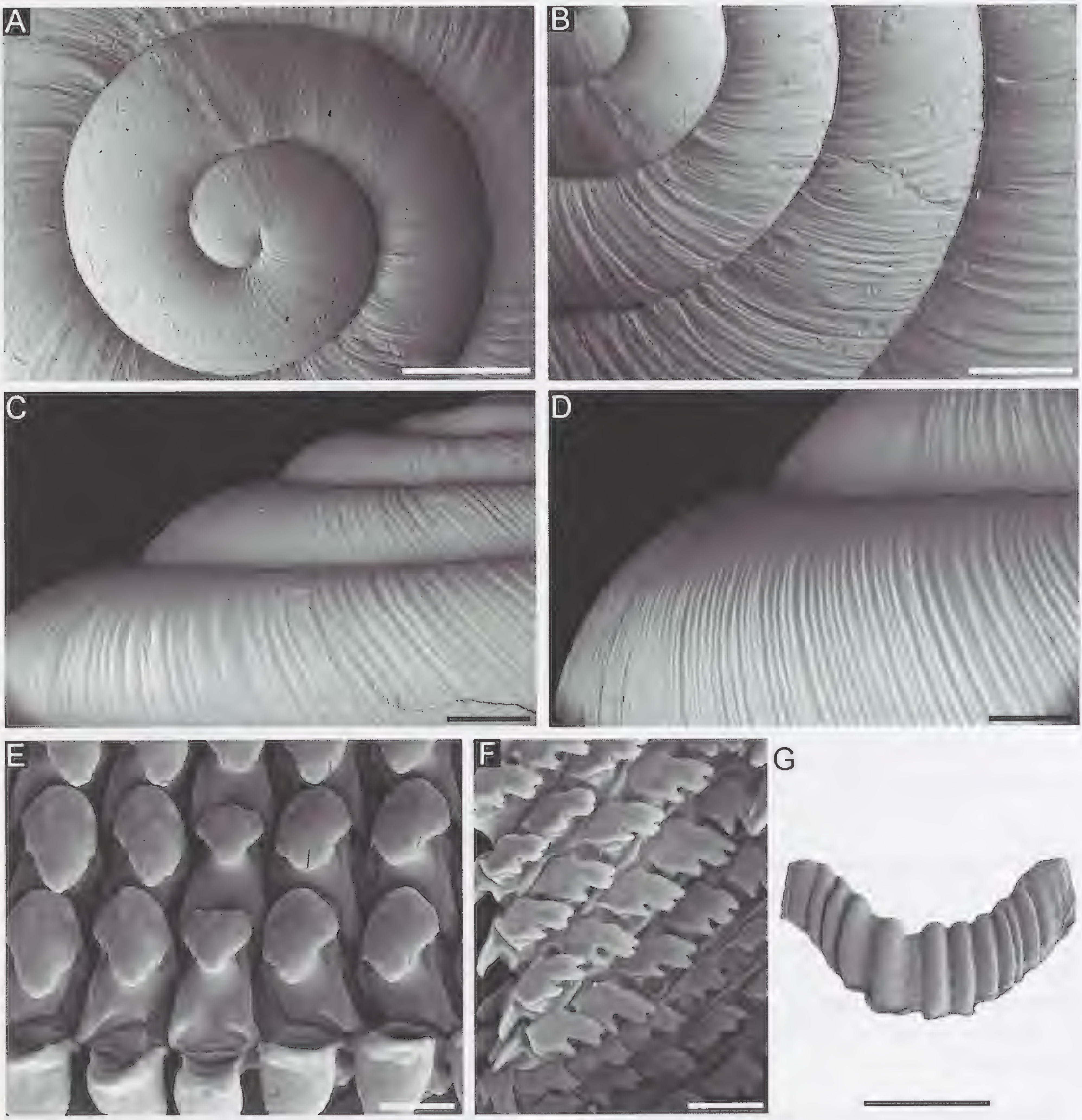

FIG. 26. SEM micrographs of ***Amplirhagada sinenomine*** n. sp. paratype WAM S37709 (unnamed island, Doubtful Bay). A–D: Shell. Scale bars = 1 mm. A: Apical view showing protoconch; B: Apical view showing sculpture on first four whorls; C: Front view showing showing sculpture on first four whorls; D: nt view showing showing sculpture on last whorl; E–F: Radula. Scale bars = 20 µm; E: Central and inner lateral teeth viewed obliquely from above; F: Marginal teeth viewed obliquely from above; G: Jaw. Scale bar = 0.5 mm.

bilicus entirely concealed; background colour brownish horn, peripheral and subsutural band usually well developed, comparatively broad, dark brown, bands may blend into each other covering entire shell surface in dark brown; surface glossy; outer and inner lip colour whitish. Protoconch 2.75 mm in diameter, comprising one whorl, smooth with delicate radial wrinkles; teleoconch smooth with faint growth lines. Angle of aperture 30 to 45°; outer lip well rounded, slightly thickened, slightly to well expanded, basal node rather small but present.

Digestive anatomy (Fig. 26E–G): Jaw consisting of 12 plates. Radula ~ 3 mm long with 126 rows of teeth (n = 1); C + 14–16 + 3–4 + 18–20.

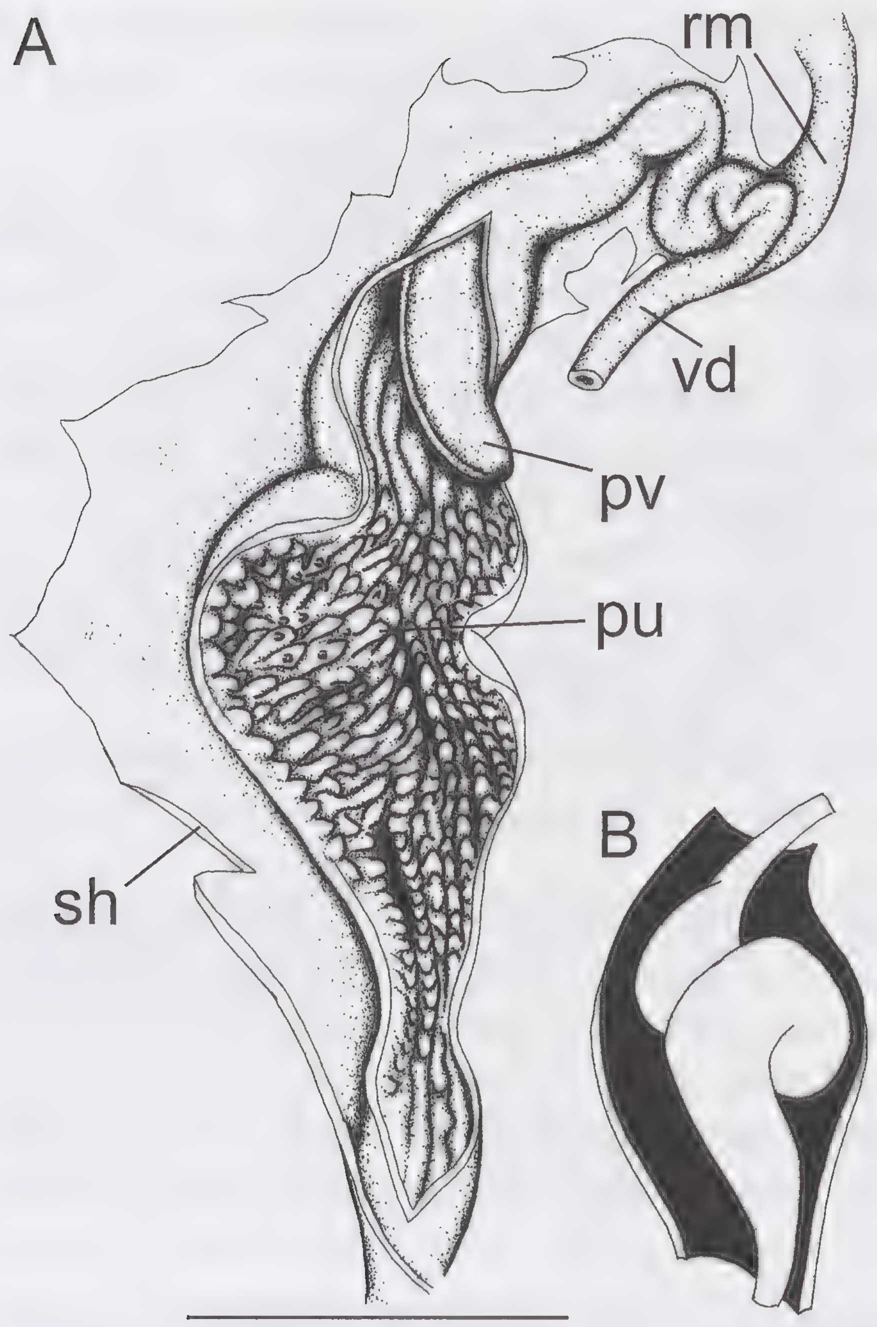

FIG. 27. Genital anatomy of ***Amplirhagada sinenomine*** n. sp. holotype WAM S37710 (unnamed island, Doubtful Bay; May). A: Internal anatomy of penis. Scale bar = 10 mm; B: Schematic representation of coiling of penis within penial sheath.

Genital anatomy (Figs. 27–28): Penis about as long as anterior part of oviduct, coiled within delicate penial sheath, vas deferens entering sheath apically; penial retractor muscle stubby; penial verge large (~ 1/5 length of penial chamber), conical, thick; penial wall entirely covered by dense pustulation, pustules comparatively large, arranged in longitudinal rows, pilasters forming at very distal and proximal end of penial wall, consisting of fused pustules; main pilaster not differentiated except that some pustules are slightly enlarged and support tiny hooks. Vagina short, distally inflated, inner vaginal wall with few, indistinct longitudinal pilasters.

Mitochondrial Differentiation

Infraspecific distance (2 sequences): 0.016; interspecific distances with respect to *A. gemina* Köhler, 2010 from near Prior Point, mainland coast about 30–40 km further north (1 sequence): 0.065–0.072, with respect to all other congeneric species (54 sequences): 0.164–0.248.

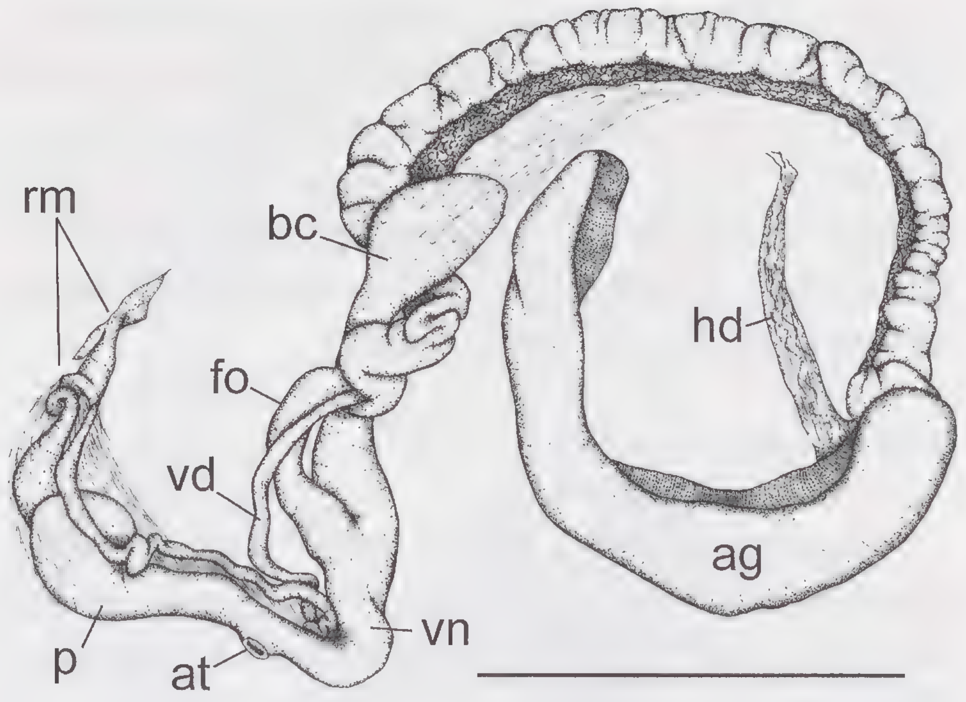

FIG. 28. Genital anatomy of ***Amplirhagada sinenomine*** n. sp. holotype WAM S37710 (named island, Doubtful Bay; May). Scale bar = 3 mm.

Comparative Remarks

Description based on dissection of one preserved specimen. Differing from *A. dubitabile* Köhler, 2010, from Steep Island, Doubtful Bay, by highly spired and nearly subglobose shell and lack of stimulatory main pilaster. Differing from other species with large, subglobose shells, such as *A. sphaeroidea*, *A. camdenensis*, ***A. globosa*** and ***A. storriana*** by presence of colour bands, whitish colour of apertural lip, completely concealed umbilicus, and typical pustulation of inner penial wall.

Distribution (Fig. 3)

Unnamed island in Doubtful Bay.

Amplirhagada storriana n. sp.

Figs. 29–31, 37A

Type Locality

Western Australia, Southwest Kimberley, Doubtful Bay, SE section of Storr Island; 15°56’54”S, 124°33’38”E; coll. Vince Kessner, 22/05/2009, KIS 3–143 (vine thicket on W-facing steep slopes, in sandstone scree).

Material Examined

Holotype WAM S58436 (preserved specimen; Fig. 37A). Paratypes AM C471721 (4 preserved specimens), WAM S37703 (4 preserved specimens), WAM S37704 (2 preserved specimens), WAM S37705 (10 preserved specimens), WAM S37706 (3 preserved specimens), WAM S37707 (3 preserved specimens), WAM S37708 (12 preserved specimens), AM C471722 (10 shells), WAM S37714 (5 shells), WAM S37715 (10 shells), WAM S37716 (21 shells), WAM S37717 (12 shells), WAM S37718 (10 shells), WAM S37819 (7 shells) from southeastern section of Storr Island.

Etymology

In honour of Glen Milton Storr (1921–1990), Curator of Ornithology and Herpetology at the Western Australian Museum, name patron of Storr Island; adjective of feminine gender.

Description

Shell (Figs. 29A, B, 37A; Table 1): Sub-globose with medium to high spire; solid; periphery angulated; upper sector convexly rounded, slightly shouldered underneath suture, basal sectors of rounded; umbilicus 80–90% concealed. Background colour yellowish brown; subsutural band absent or diffuse, brown; peripheral band varying in thickness and contrast, usually diffuse, brown, visible on last whorl(s) only; bands usually blending into each other across whorl surface; ventral colour whitish or identical with background; inner and outer lip colour blending into dark purplish brown. Protoconch ~ 2.9 mm in diameter, comprising about one whorl, essentially smooth with faint axial lirae. Teleoconch with fine, indistinct axial growth lines, becoming oblique towards base of shell. Angle of aperture 30–45°; outer lip rounded, slightly expanded, not or weakly reflected, basal node of lip weak, palatal node absent.

Radula (Fig. 29 C–D): 3.8 x 1.3 mm in size, with about 130 rows of teeth (n = 1); C + 12–13 + 4 + 18–19.

Genital anatomy (Figs. 30–31): Penis rather straight, slightly longer than anterior part of oviduct, thin, penis proper comprising proximal third only. Vas deferens relatively thick, forming elongated loop before entering penis, uncoiled. Penial retractor muscle very short. Penial

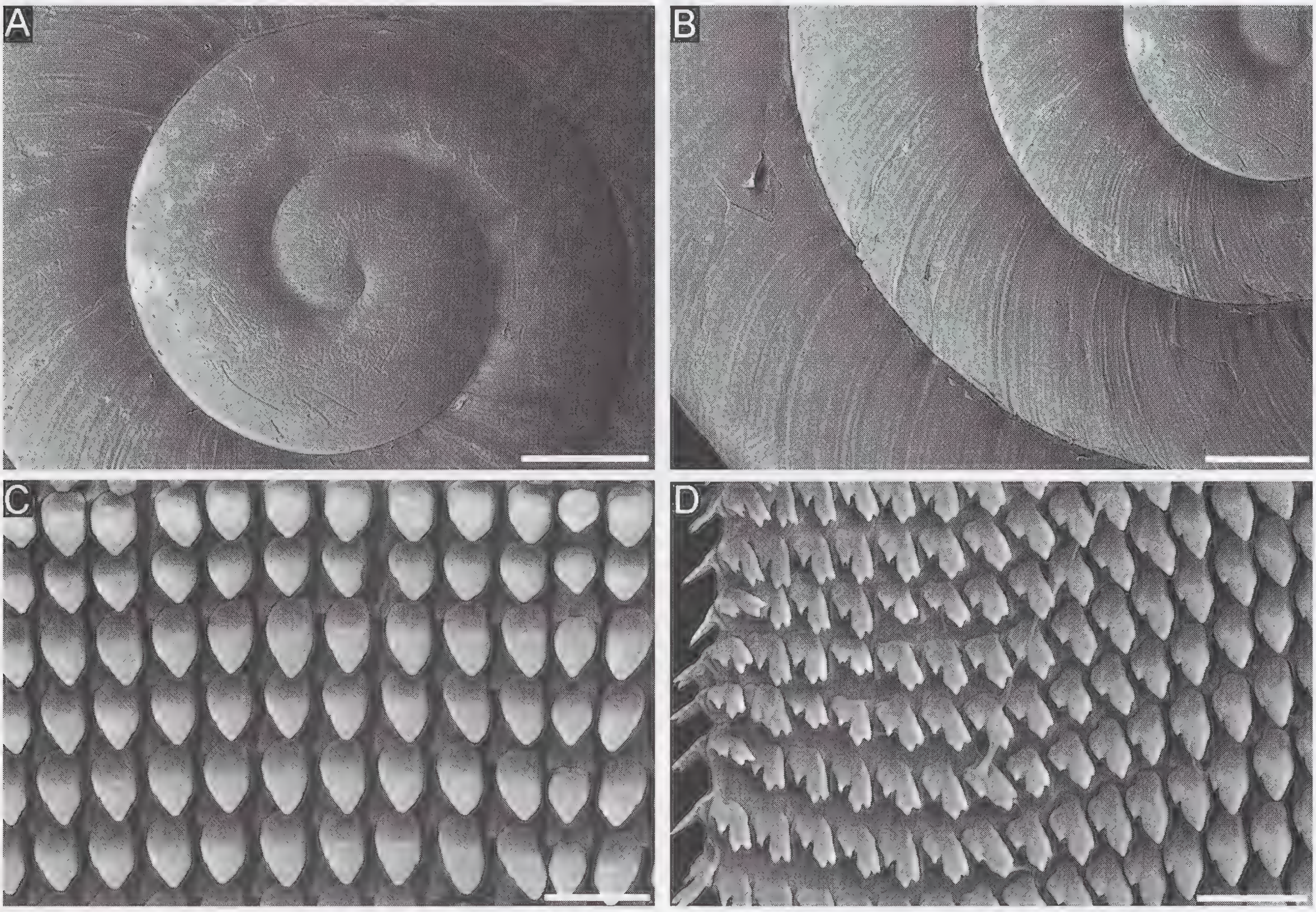

FIG. 29. SEM micrographs of ***Amplirhagada storriana*** n. sp. (Storr Island). A–B: Shell, paratype WAM S37703. Scale bars = 1 mm. A: Apical view showing protoconch; B: Apical view showing sculpture on first four whorls; C–D: Radula, paratype WAM S37708. Scale bars = 50 µm. C: Central and inner lateral teeth viewed from above; D: Middle marginal and outer lateral teeth viewed from above.

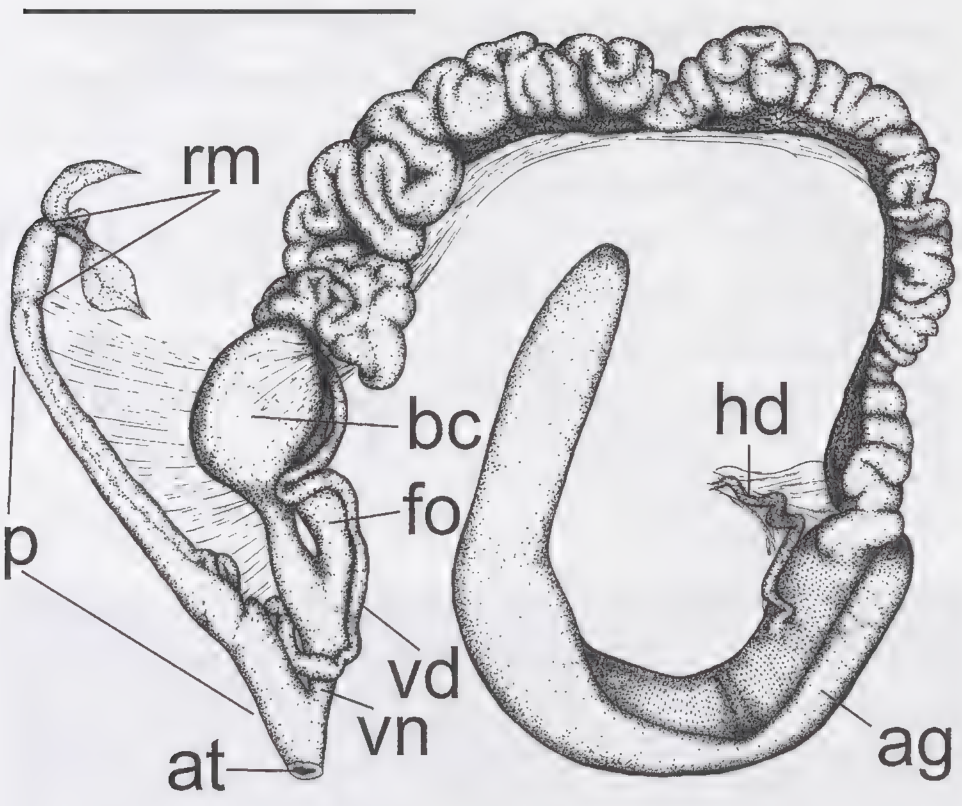

FIG. 30. Genital anatomy of ***Amplirhagada storriana*** n. sp. paratype AM C471721 (Storr Island; May). Scale bar = 10 mm.

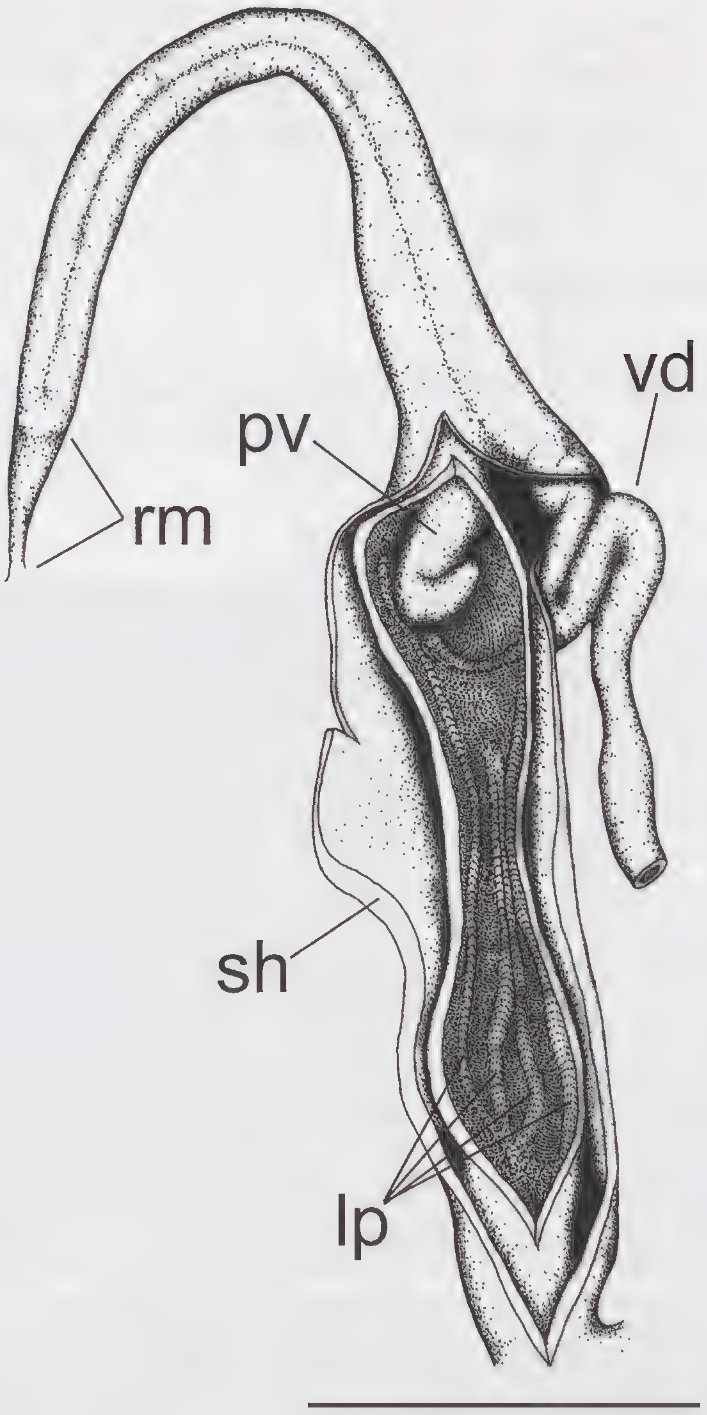

FIG. 31. Penial anatomy of ***Amplirhagada storriana*** n. sp. paratype AM C471721 (Storr Island; May). Scale bar = 3 mm.

verge short, slender, with pointed tip. Penial wall without pustulation; no main stimulatory pilaster differentiated; four narrow longitudinal pilasters form along entire length of inner penial wall. Vas deferens entering penial sheath at distal third.

Aestivation Strategy

Free sealer, under rocks.

Mitochondrial Differentiation

Infraspecific distance (2 sequences): 0.016; interspecific distances with respect to *A. sphaeroidea* (2 sequences): 0.102–0.107, to *A. regia* (2 sequences): 0.117–0.121, to *A. camdenensis* (1 sequence): 0.107–0.114, to *A. basilica* (1 sequence): 0.134–0.138, all other congeneric species (49 sequences): 0.184–0.254.

Comparative Remarks

One of the species with dome-shaped shells; shell most similar to *A. uwinsensis*; proportionally taller than most other species (H/D = 0.87), including *A. uwinsensis* (0.72), *A. sphaeroidea* (0.68), *A. regia* (0.71), *A. basilica* (0.68) and ***A. globosa*** (0.68). A similar size ratio in *A. camdenensis* (0.85) and *A. decora* (0.89), while *A. boongareensis* is even taller (0.97) (Table 1). *Amplirhagada camdenensis* is smaller in overall size with a comparatively higher body whorl while *A. decora* differs in banding of shell, lighter background and whitish outer lip; *A. tricenaria* and *A. regia* differ by dark brown outer lip. Penial anatomy of ***A. storriana*** resembles most closely that of *A. basilica* and, to a lesser degree, of *A. camdenensis* but differing in details of development of longitudinal pilasters. *Amplirhagada uwinensis* differs most conspicuously by presence of large main stimulatory pilaster, *A. sphaeroidea* by presence of oblique lateral lamellae, *A. regia* by shorter and fewer longitudinal pilasters, *A. boongareensis* and *A. tricenaria* by presence of pustulation and main stimulatory pilaster.

Distribution (Fig. 3)

Storr Island.

Amplirhagada alkuonides n. sp.
Figs. 32–34, 37B

Type Locality

Western Australia, SW Kimberley, Buccaneer Archipelago, Collier Bay, Woods Islands, Kingfisher Island; 16°05'21.8"S, 124°05'34.3"E; coll. Vince Kessner, 5/0602009, KIS 3–173 (vine thicket behind mangrooves on rocky substratum, common).

Material Examined

Holotype WAM S58435 (preserved specimen; Fig. 37B). Paratypes AM C471718 (20 preserved specimens), WAM S37717 (50 preserved specimens), WAM S37718 (37 preserved specimens), AM C471719 (38 shells), WAM S37828 (100 shells) from Kingfisher Island.

Additional, non-type material AM C471720 (preserved specimens), WAM S37712–6, WAM S49247–8 (preserved specimens), WAM S37825, WAM S37827 (shells) from Kingfisher Island.

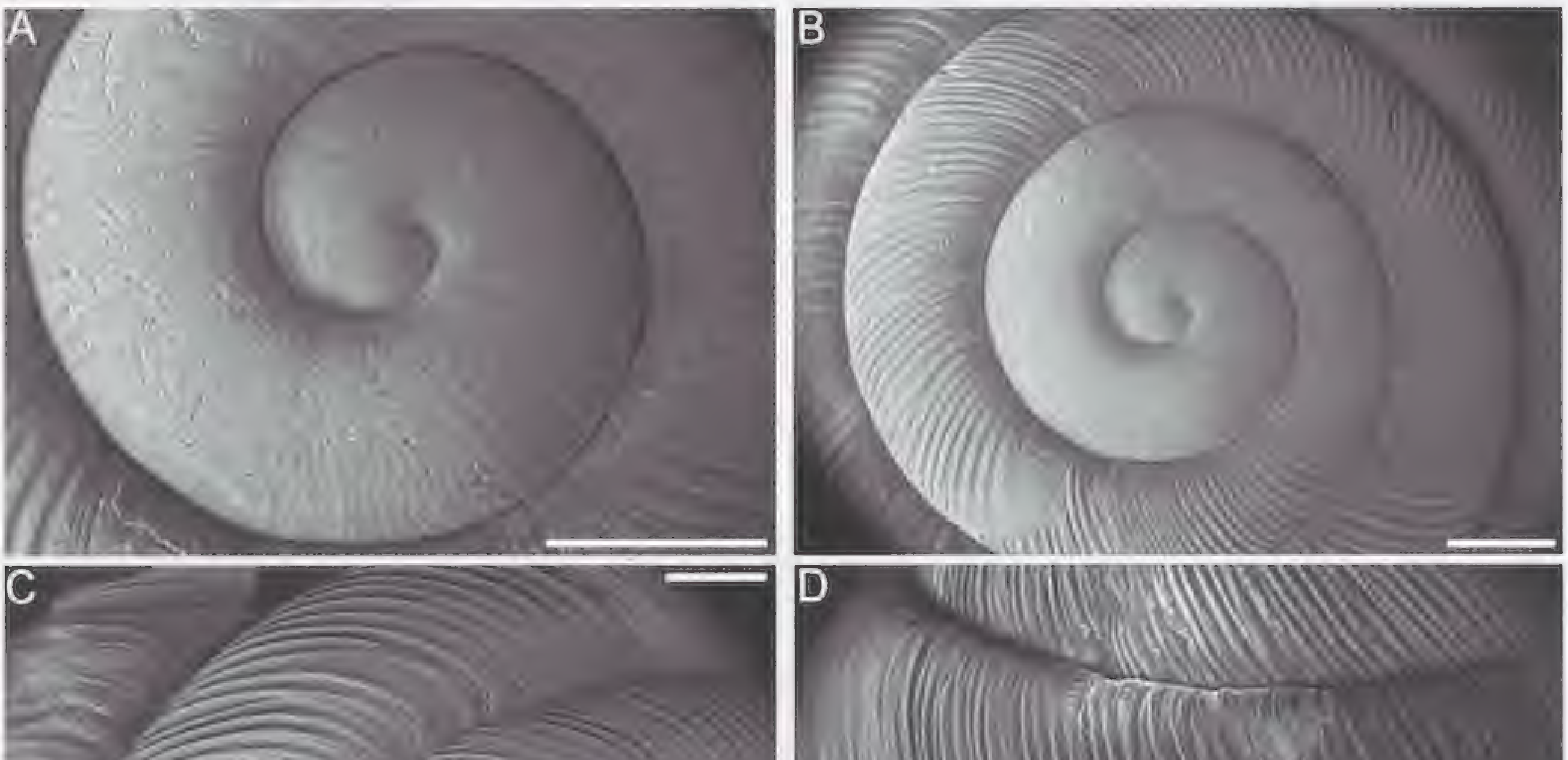

FIG. 32. SEM micrographs of ***Amplirhagada alkuonides*** n. sp. paratype AM C471718 (Kingfisher Island). A–D: Shell. Scale bars = 1 mm. A: Apical view showing close-up of protoconch; B: Apical view showing first whorls; C: Apical view showing sculpture on last whorls; D: Lateral view showing sculpture on body whorl; E–F: Radula. Scale bars = 50 µm. C: Central and inner lateral teeth viewed from above; D: Middle marginal and outer lateral teeth viewed from above.

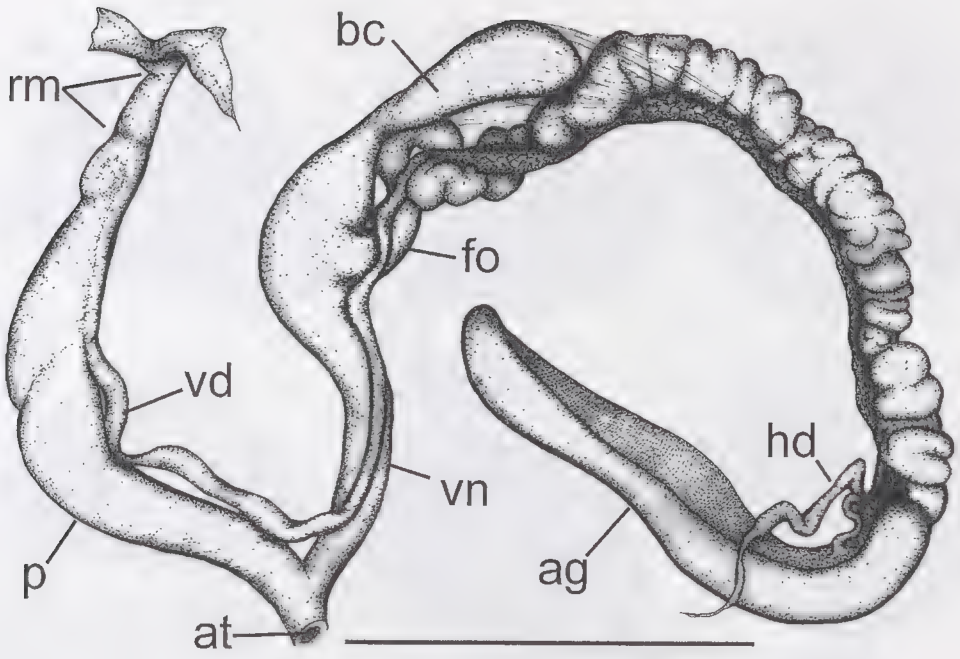

FIG. 33. Genital anatomy of ***Amplirhagada alkuonides*** n. sp. paratype AM C471718 (Kingfisher Island; June). Scale bar = 10 mm.

Etymology

Derived from the Greek word ἀλκυών (alkuōn = kingfisher). The feminine suffix "-ides" comes from ειδος (eidos), meaning "type" or "kind"; referring to the name of Kingfisher Island; adjective of feminine gender.

Description

Shell (Figs. 32A–D, 37B; Table 1): Broadly conical with low spire; thin (translucent) but solid; periphery well rounded to slightly angulated, upper and basal sectors of whorls rounded; umbilicus 50–90% concealed. Background and ventral colour whitish crème to horn; peripheral and subsutural bands well marked, brown, visible on basal whorls; outer and inner lip colour white. Protoconch 2.9 mm in diameter, comprising about one whorl, sculptured by very indistinct axial pustulation. Teleoconch with well developed, regularly spaced axial ribs, evenly distributed across entire surface of shell, reduced in prominence below suture. Angle of aperture ~ 45°; outer lip moderately thick, well rounded, expanded, not or weakly reflected; basal node weak, palatal node absent.

Radula (Fig. 32E, F): 4.3 mm long, with 125 rows of teeth; C + 14–16 + 4 + 12–14 (n = 2).

Genital anatomy (Figs. 33–34): Penis long, tubular, coiled within delicate penial sheath, vas deferens entering sheath in distal third; penial wall thick, penial verge elongately conical with rounded tip, 1/10 to 1/8 of length of penial chamber; penial wall entirely covered with very fine and dense pustulation, pustules small, elongated, with rounded tip, arranged in longitudinal rows, main stimulatory pilaster weakly differentiated, comprising apical third of penial wall, densely covered by pustules. Vagina considerably elongated, tubular. Bursa copulatrix long, considerably extending base of spermoviduct; with inflated head, inner wall with many irregular, rather narrow longitudinal pilasters. Spermoviduct much longer than anterior part of oviduct.

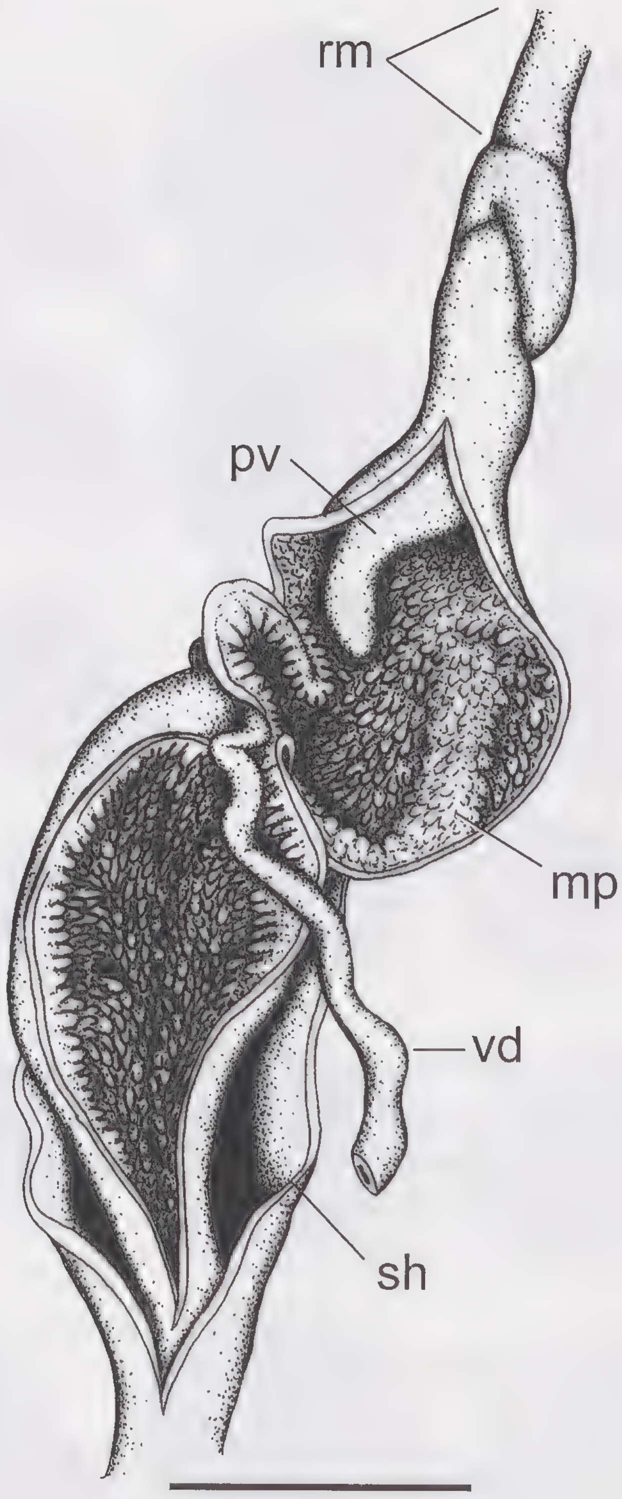

FIG. 34. Penial anatomy of ***Amplirhagada alkuonides*** n. sp. paratype AM C471718 (Kingfisher Island; June). Scale bar = 3 mm.

Aestivation Strategy

Free sealer.

Mitochondrial Differentiation

Infraspecific distance (2 sequences): 0.012; interspecific distances with respect to *A.* cf. *astuta* from Molema Island: 0.051, to all other congeneric species (56 sequences): 0.166–0.255.

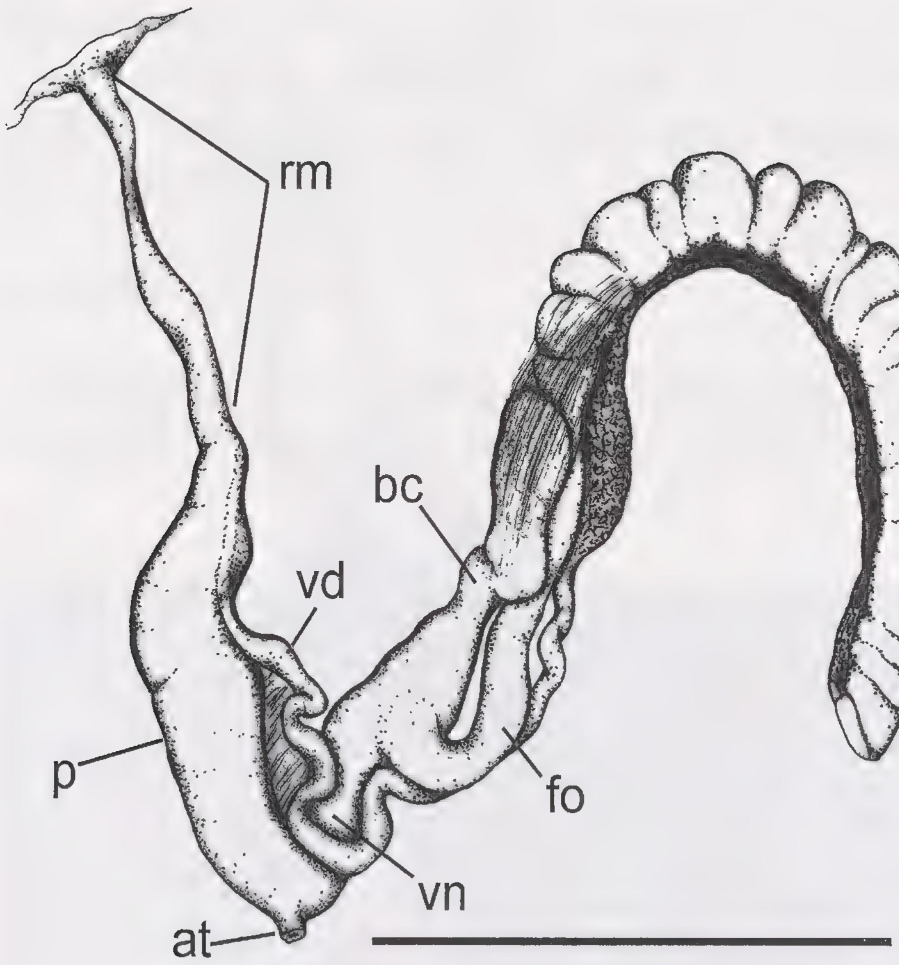

FIG. 35. Genital anatomy of *Amplirhagada* cf. *astuta* (WAM S49262, Molema Island; February). Distal part of spermoviduct with albumen gland ripped off. Scale bar = 10 mm.

Comparative Remarks

Anatomical description based on dissection of two specimens. Specimens with nearly identical shells were found on Melomys Island (Woods Island group, less than 10 km south of Kingfisher Island), considered conspecific. Specimens from mainland (Walcott Inlet, 1 km from coast, 16°21'20"S, 124°45'55"E), identified by Solem as "*Amplirhagada* NSP37" (housed in FMNH), have similar shells; their status being under investigation. Shells of ***A. alkuonides*** resemble none of the species from other islands in southern part of the Kimberley coast, which usually exhibit subglobose to dome-like shells. Similar to species that occur much further north, such as *A. indistincta* and *A. solemiana*. These species differ by presence of several longitudinal pilasters that form along entire inner surface of inner penial wall. The elongated bursa copulatrix, which considerably extends anterior end of spermoviduct is diagnostic.

Distribution (Fig. 3)

Woods Island group, on Kingfisher and Melomys islands.

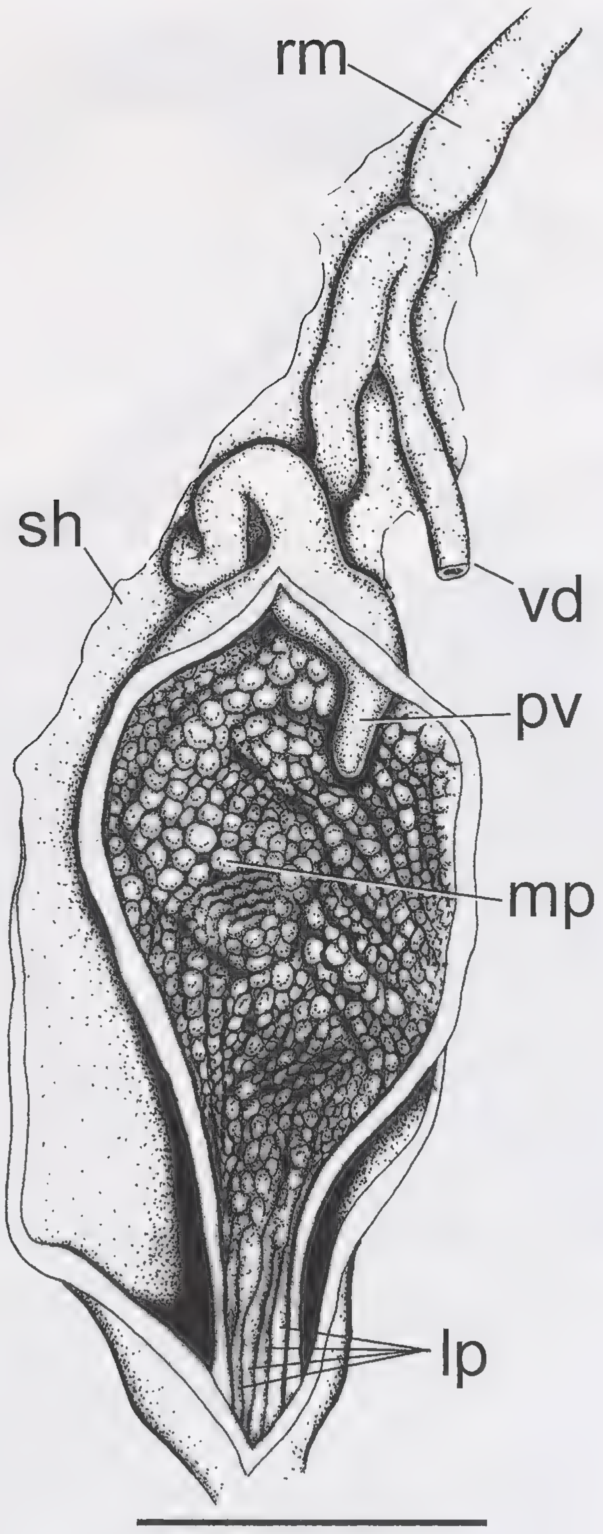

FIG. 36. Penial anatomy of *Amplirhagada* cf. *astuta* (WAM S49262, Molema Island; February). Scale bar = 3 mm.

Amplirhagada cf. *astuta* (Iredale, 1939)

Figs. 35, 36, 37C

Rhagada astuta Iredale, 1939: 63, pl. IV, fig. 17.
Amplirhagada astuta – Solem, 1981a: 208–211, Fig. 46; McKenzie et al., 1995: 251.

Type Locality

Western Australia, southwest Kimberley, Yampi Sound, Koolan Island (16°08'S, 123°45'E).

Taxonomic Remarks

The name was introduced by Iredale (1939) based on a leached and worn shell as member of *Rhagada*. Subsequently transferred to *Am-*

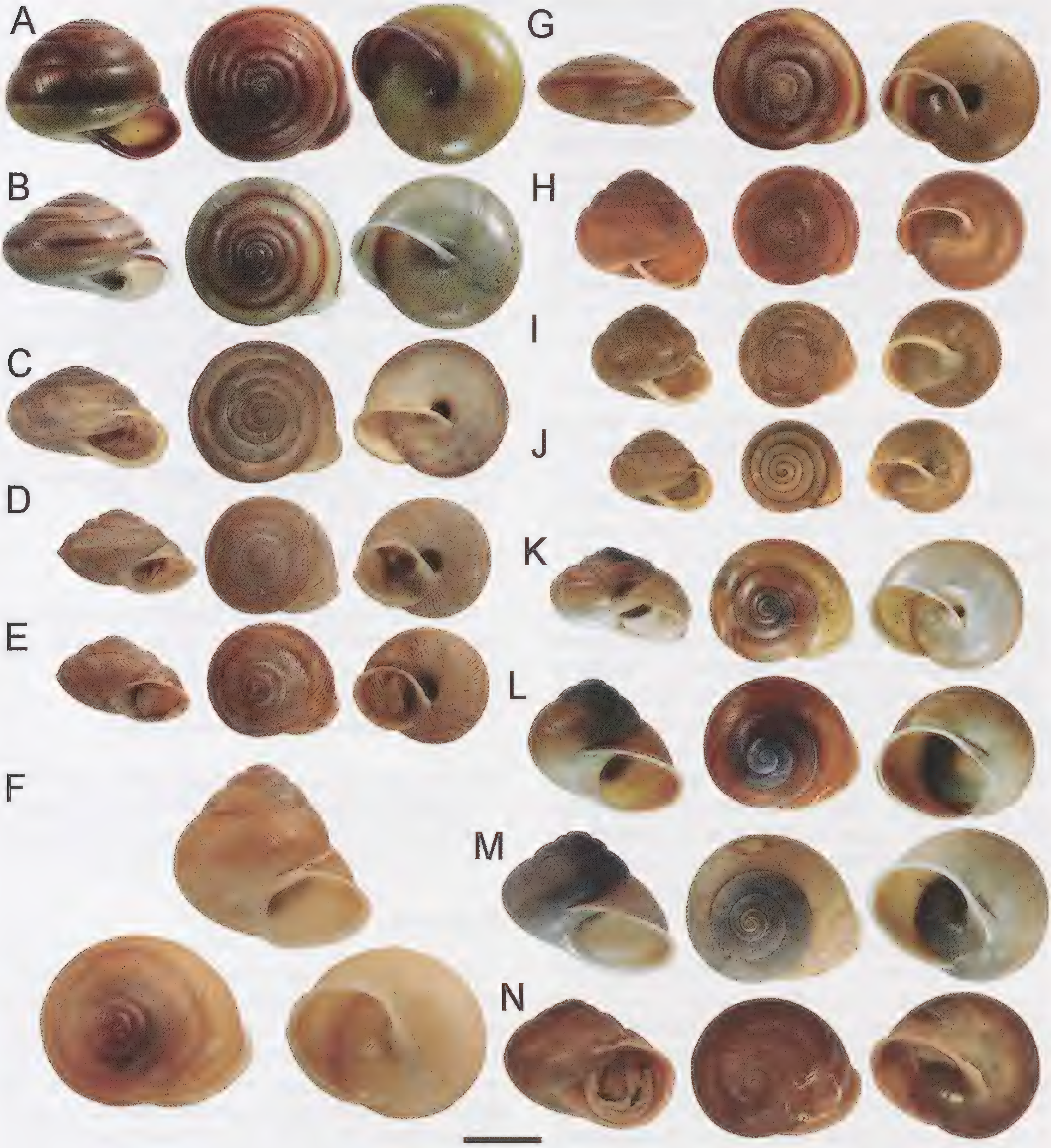

FIG. 37. Shells of *Amplirhagada* (continued), *Carinotrachia*, *Kimberleymelon*, *Kimberleydiscus*, and *Kimboraga*. A: ***A. storriana*** n. sp. holotype WAM S58436 (Storr Island); B: ***A. alkuonides*** n. sp. holotype WAM S58435 (Kingfisher Island); C: *A. astuta* WAM S37808 (Molema Island). D: *Carinotrachia admirale admirale* holotype WAM S34628 (Middle Osborn Island); E: *Carinotrachia admirale elevata* holotype WAM S34629 (Southwest Osborn Island); F: *Kimberleymelon tealei* holotype WAM S36877 (Middle Osborn Island); G: *Kimberleydiscus fasciatus* holotype WAM S34630 (Bigge Island); H: *Australocosmica augustae* holotype WAM S34667 (Augustus Island); I: *Australocosmica sanctumpatriciusae* holotype WAM S34666 (St Patrick Island); J: *Australocosmica vulcanica* holotype WAM S34668 (unnamed island, Vulcan Group); K: ***Kimboraga glabra*** n. sp. holotype WAM S58437 (Coronation Island); L: *Kimboraga exanima* WAM S37622 (St Andrews Island); M: ***Kimboraga wulalam*** n. sp. holotype WAM S58438 (Wulalam Island); N: ***Kimboraga cascadensis*** n. sp. holotype WAM S58439 (Lachlan Island). Note that foot tissue protrudes from some shells. Scale bar = 10 mm.

plirhagada by Solem (1981a), who considered it a *nomen nudum* for lack of information that would permit its recognition. Later observations confirmed existence of *A. astuta* on Koolan Island (McKenzie et al., 1995). Because occurrence on Molema Island, about 20 km SW of Koolan Island, is considered likely, present material is assigned to this name and used to redescribe the taxon. A final evaluation of the status of the Molema Island samples with respect to the type material awaits comparative analyses of topotypic material.

Material Examined

WAM S49262 (preserved animal without shell), WAM C37808 (shell) from Talbot Bay, northern section of Molema Island, 16°14'17.4"S, 123°49'49.5"E.

Description

Shell (Fig. 37C; Table 1): Broadly conical with low spire; thin (translucent) but solid; periphery well rounded, upper and basal sectors of whorls rounded; 10% concealed. Background and ventral colour whitish crème to horn; peripheral and subsutural bands well marked, brown, visible on basal whorls; outer and inner lip colour white. Teleoconch with faint, regularly spaced axial growth lines, evenly distributed across entire shell surface. Angle of aperture ~ 45°; outer lip sharp, well rounded, strongly expanded, weakly reflected; basal node weak, palatal node absent.

Genital anatomy (Figs. 35–36): Penial complex elongate, with bulbous proper, not coiled within penial sheath, vas deferens entering sheath in distal third of penial complex; verge elongate to narrowly conical with rounded tip, < 1/10 of length of penial chamber; penial wall entirely covered with dense pustulation, pustules moderate in size, roundish, arranged in irregular, obliquely longitudinal rows, main stimulatory pilaster weakly differentiated, comprising distal third of penial wall, consisting of lateral, corrugated lamellae formed by fused pustules; proximal portion of inner wall with weak longitudinal pilasters. Vagina short, inflated, inner wall with weak longitudinal pilasters. Bursa copulatrix long, slightly extending base of spermoviduct; head inflated, inner wall with many irregular, rather narrow longitudinal pilasters. Spermoviduct longer than anterior part of oviduct.

Mitochondrial Differentiation

Interspecific distances with respect to ***A. alkuonides*** (2 sequences): 0.051, to all other congeneric species (56 sequences): 0.186–0.241.

Comparative Remarks

Shells from Molema Island exhibit corresponding features with the holotype (flat and broad shape, partly open umbilicus, expanded lip, smooth sculpture, and number of whorls). Compared to ***A. alkuonides*** from Kingfisher Island, ~ 25 km NE of Molema Island, *A. astuta* has a flatter, smoother shell, entirely open umbilicus, more expanded apertural lip; genital anatomy differing by larger, more rounded pustules, proportionally shorter vagina and bursa copulatrix.

Distribution (Fig. 3)

Kooland Island, Yampi Sound, and Molema Island, Talbot Bay; occurrence on adjacent mainland likely.

Carinotrachia Solem, 1985

Carinotrachia Solem, 1985a: 857–863; 1991: 214; Solem & McKenzie, 1991: 247–263; Köhler, 2010b: 2–6. Type species: *Carinotrachia carsoniana* Solem, 1985, by original designation.

Diagnosis

Shell: Medium sized (D = 15.5–18.5 mm), moderately thick, broadly conical, moderately elevated; umbilicus narrowly open; protoconch with strong radially elongated pustulation; teleoconch sculptured by strongly developed radial ribs, ribs extending onto base of shell, microscopic granulation may be present; whorls rapidly increasing, separated by deep suture; periphery keeled. Shell colour uniform, yellowish brown.

Genital anatomy: Penis with well-developed sheath, extending entire length, usually thick proximally, thin distally; inner penial wall with complex pilasters; epiphallus absent; penial retractor muscle attached to junction with vas deferens. Vas deferens entering penial sheath apically, entering penial chamber through simple pore. Bursa copulatrix simple, short (slightly extending anterior end of spermoviduct).

Radula: 3.5–5.5 mm long, with 120–140 rows of teeth, tooth formula: C + 12–14 + 3–4 + 13–15.

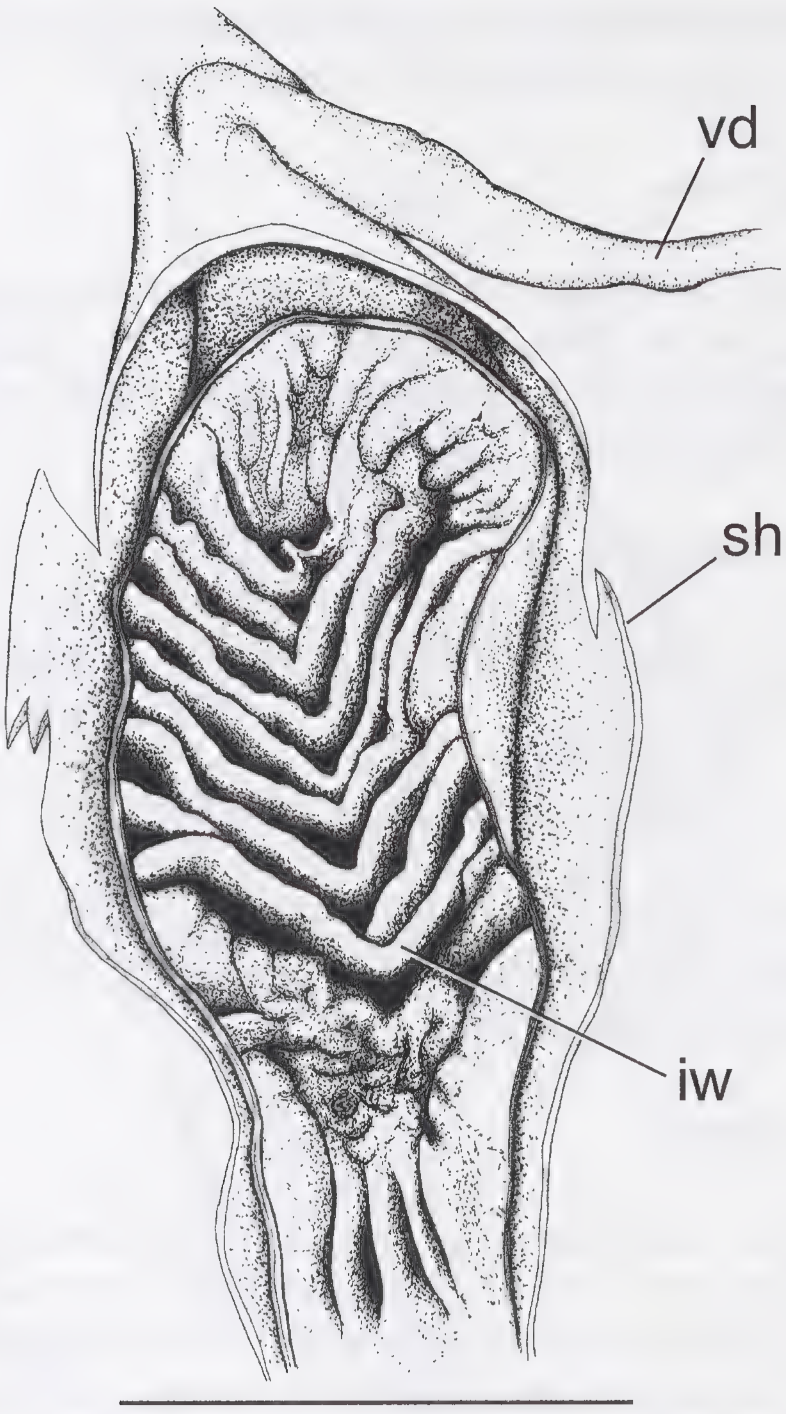

FIG. 38. Penial anatomy of *Carinotrachia admirale admirale* (AM C463606, Middle Osborn Island; May). Scale bar = 3 mm.

Aestivation Strategy

Rock sealer (Solem, 1985; Köhler, 2010b).

Diversity and Distribution

Two species are currently known: The type species, *C. carsoniana* from south of Kalumburu on the mainland and *C. admirale* with each a distinct subspecies on Middle and Southwest Osborn islands, respectively, about 60 to 80 km W of Kalumburu.

Carinotrachia admirale admirale
Köhler, 2010
Figs. 37D, 38

Carinotrachia admirale admirale Köhler, 2010b: 3–6, figs. 2A, 3–5.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, E coast of Middle Osborn Island, 14°18’57.1”S, 126°01’59.6”E.

Material Examined

Holotype WAM S34628 (preserved specimen; Fig. 37D). Paratypes AM C463606 (32 preserved specimens), WAM S36600 (100 preserved specimens) from type locality.

Diagnosis

Shell: Thin, strongly depressed, with about four regularly expanding whorls, strongly keeled periphery, upper part of whorl slightly shouldered, basal part convexly flattened; umbilicus narrowly open, 20% concealed; uniform crèmish brown to horn; sculptured by regularly-spaced, rounded, prosocline axial ribs, reduced in prominence below suture and within umbilicus, spaces between ribs about twice as wide as thickness of the ribs, minute periostracal nodules sparsely distributed on last one to two whorls, but dense on basal part of shell and within umbilicus; outer lip well rounded, sharp, without parietal or basal notch (Fig. 37D).

Genital anatomy: Inner penial wall covered with dense pilasters in irregular fishbone-pattern, no stimulatory main pilaster (Fig. 38).

Comparative Remarks

Similar to *C. carsoniana* Solem, 1985, with respect to shell shape, size and sculpture but differing by presence of small nodules on shell surface, which are largely absent in *C. carsoniana*, more rounded shape of ribs, comparatively larger distances between ribs, and in anatomy of inner penial wall (*C. carsoniana* with much more irregularly arranged pilasters). In *C. carsoniana* vas deferens communicates with lumen of penis through valvular ridge; in *C. admirale* through simple pore.

Distribution

Middle Osborn Island, in rainforest patches.

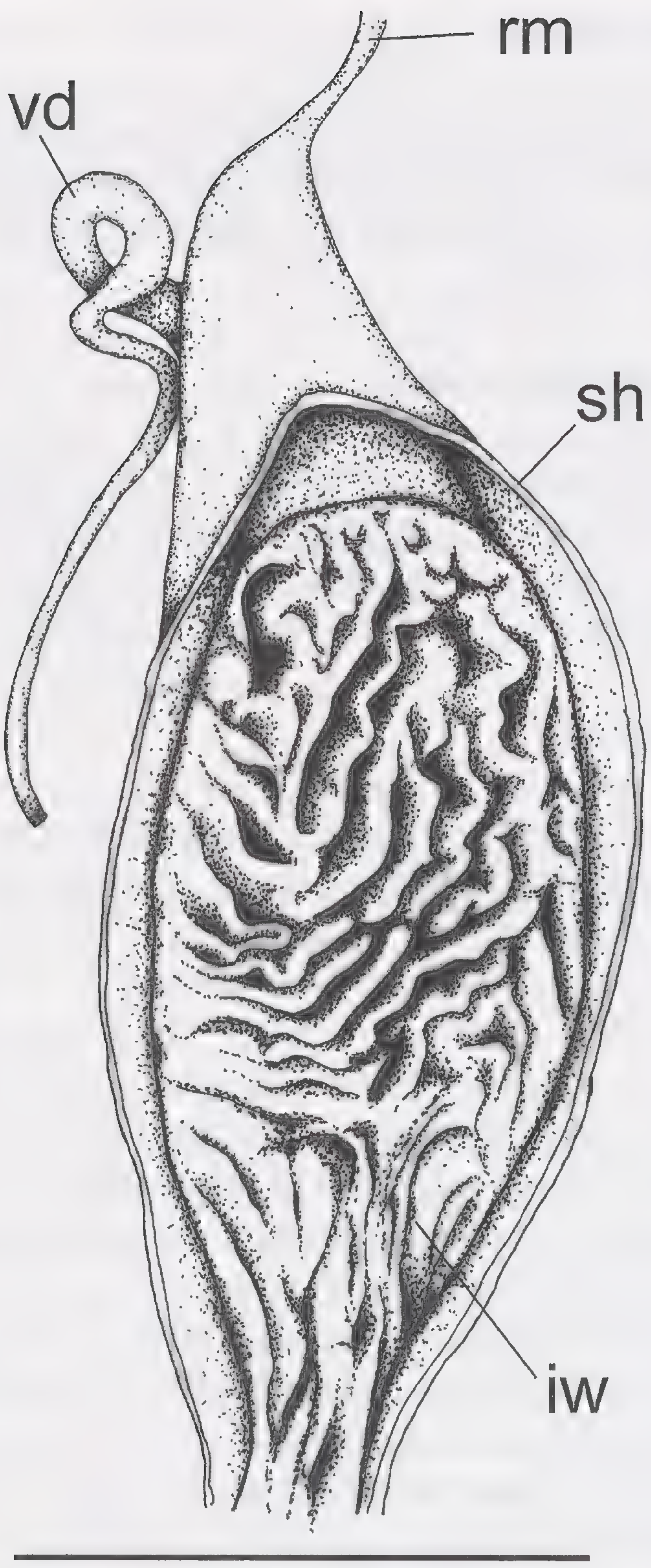

FIG. 39. Penial anatomy of *Carinotrachia admirale elevata* (AM C463607, Southwest Osborn Island; May). Scale bar = 3 mm.

Carinotrachia admirale elevata
Köhler, 2010
Figs. 37E, 39

Carinotrachia admirale elevata Köhler, 2010b: 3–6, figs. 2B, 6–8.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, E coast of Southwest Osborn Island, 14°22’47.3”S, 125°56’00.6”E.

Material Examined

Holotype WAM S34629 (preserved specimen; Fig. 37E). Paratypes AM C463607 (10 preserved specimens), WAM S36857 (27 preserved specimens) from type locality.

Diagnosis

Like nominate form but with weaker spiral keel, more elevated spire (Fig. 37E), more irregularly arranged pilasters on the inner penial wall (Fig. 39).

Distribution

Southwest Osborn Island, in rainforest patches.

Kimberleymelon Köhler, 2010

Kimberleymelon Köhler, 2010b: 6–9. Type species: *Kimberleymelon tealei* Köhler, 2010, by original designation.

Diagnosis

Shell: Comparatively large, trochiform, high-spired, moderately thick; umbilicus completely concealed; protoconch rather smooth with faint radial growth lines; teleoconch with prominent radial growth lines, extending onto base of shell; whorls rapidly increasing, separated by flat suture; periphery slightly depressed.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; inner penial wall with pustulation and well-developed main pilaster; epiphallus wanting, simple, tubular reflection of vas deferens; penial retractor muscle attached to junction of epiphallus with vas deferens. Vas deferens entering penial sheath apically, epiphallus entering penial chamber through indistinct vergic papilla. Bursa copulatrix simple, short (reaching anterior end of spermoviduct).

Aestivation Strategy

Rock sealer.

Diversity and Distribution

This monotypic genus is known from Middle Osborn Island only.

Kimberleymelon tealei Köhler, 2010
Figs. 37F, 40

Kimberleymelon tealei Köhler, 2010b: 8–12, Figs. 2D, 9–11.

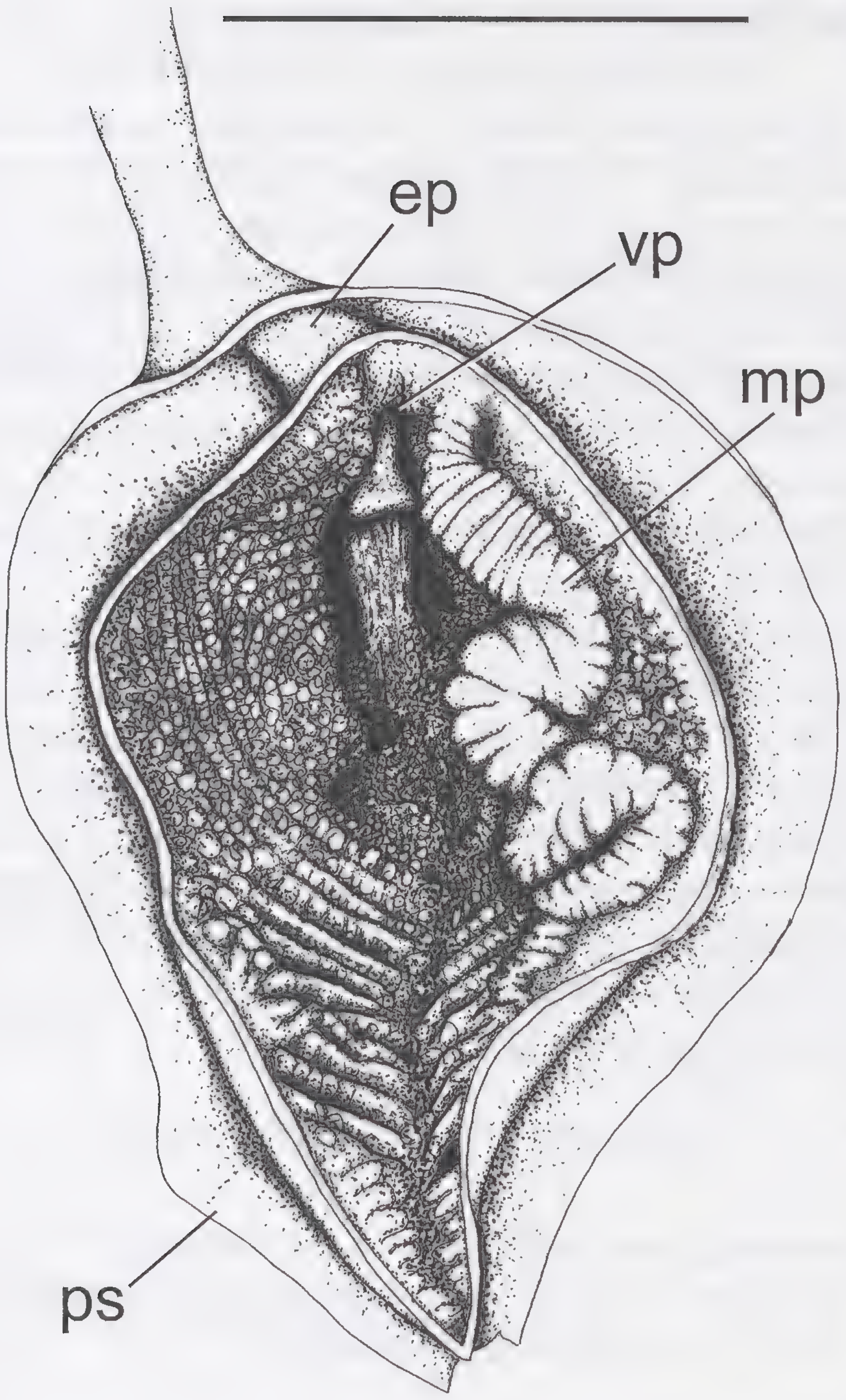

FIG. 40. Penial anatomy of *Kimberleymelon tealei* (WAM S36877, Middle Osborn Island; August). Scale bar = 5 mm.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, W coast of Middle Osborn Island, 14°18'27.3"S, 125°59'24.7"E.

Material Examined

Holotype WAM S36877 (preserved specimen; Fig. 37F). Paratypes AM C463610 (3 shells), WAM S36489 (4 shells) from 14°18'27.3"S, 125°59'24.7"E; WAM S36490 (shell) from 14°18'37.4"S, 125°59'18.4"E; WAM S36488 (shell) from 14°18'40.0"S, 126°01'29.4"E.

Diagnosis

Shell: (H = 18.3–26.4 mm), whitish colour with diffuse brownish subsutural and peripheral bands that may blend into each other to cover surface of shell in a light brown tone; apertural lip well rounded, moderately thick, slightly expanded but not reflected; parietal callus well developed, basal and palatal nodules absent (Fig. 37F).

Radula: 3.5–5.5 mm long with 180 rows of teeth; C + 17 + 2 + 25.

Genital anatomy: Penis straight, longer than anterior part of oviduct; penial retractor muscle stubby; inner penial wall with small pilaster next and anterior to vergic papilla, very fine, dense pustulation in fishbone-pattern on entire length of inner penial wall, increasing in size towards anterior base; main stimulatory pilaster well developed, corrugated, undulating, comprising apical to median portion of inner penial wall (Fig. 40). Vagina moderately long, inner wall with densely packed, corrugated longitudinal pilasters.

Comparative Remarks

There are only a few species with similarly large shells, such as *Xanthomelon* and *Globorhagada*. These differ by more globular shell shape, lower spire, yellowish to dark brown colour, much longer penial retractor muscle, lack of epiphallus, and lack of anatomy of main stimulatory pilaster of inner penial wall.

Kimberleydiscus Köhler, 2010

Kimberleydiscus Köhler, 2010b: 10–14. Type species: *Kimberleydiscus fasciatus* Köhler, 2010, by original designation.

Diagnosis

Shell: Comparatively large, discoid, low-spired, moderately thick; umbilicus almost not concealed; protoconch rather smooth with faint radial growth lines; teleoconch with fine radial growth lines, extending onto base of shell; whorls rapidly increasing, flat suture; periphery angulated.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; inner penial wall with pustulation and well-developed main pilaster; epiphallus wanting, simple (= tubular reflection of vas deferens); penial retractor muscle attached to junction of epiphallus with vas deferens. Vas deferens entering penial sheath apically, epiphallus entering penial chamber through simple pore. Bursa copulatrix simple, reaching anterior end of spermoviduct.

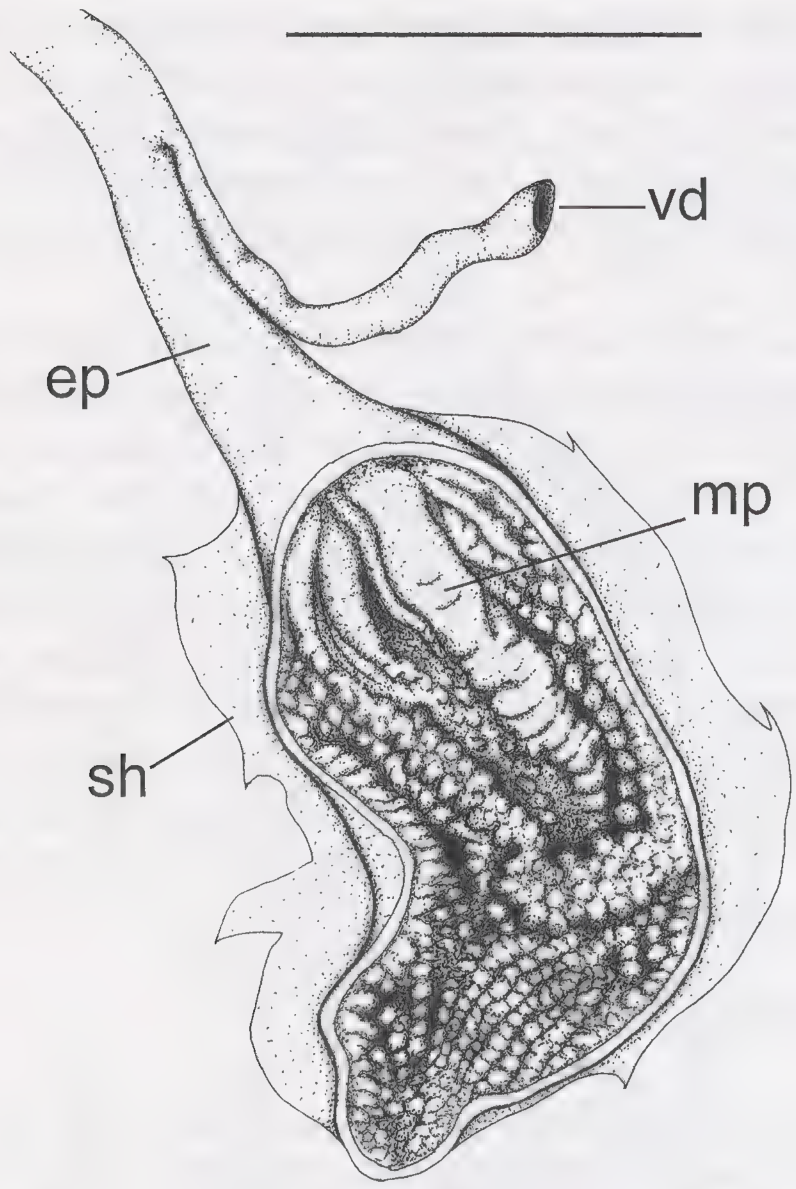

FIG. 41. Penial anatomy of *Kimberleydiscus fasciatus* (AM C463606, Bigge Island; February). Scale bar = 5 mm.

Diversity and Distribution

This monotypic genus is known from Bigge Island only.

Kimberleydiscus fasciatus Köhler, 2010

Figs. 37G, 41

Kimberleydiscus fasciatus Köhler, 2010b: 12–14, figs. 2C, 12–14.

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Bigge Island, 4.4 km NNE of Savage Hill, 14°35”13’S, 125°11’10.5”E.

Material Examined

Holotype WAM S34630 (preserved specimen; Fig. 37G). Paratypes AM C463606 (3 preserved specimens), WAM S36869 (9 preserved specimens) from type locality; WAM S36868 (preserved specimen) from 14°35’20.5”S, 125°11’06.8”E; WAM S36630 (preserved specimen), AM C463608 (5 shells), WAM S36486 (10 shells) from 14°35’33”S, 125°11’19”E.

Diagnosis

Shell: 18–22 mm in diameter, umbilicus comprising 13–20% of shell diameter, 5–20% concealed; colour horn, subsutural and peripheral bands well defined, rather broad, reddish brown; outer lip colour paler than shell; apertural lip simple, sharp, expanded, slightly reflected, parietal callus thin, no basal or palatal nodules (Fig. 37G).

Radula: 3.2–4.5 mm long with 110–140 rows of teeth; C + 13–14 + 3–4 + 20–21.

Genital anatomy: Penis slightly contorted, penial retractor muscle about as long as penis; inner penial wall with conspicuous pustulation, pustules moderate in size, densely arranged in longitudinal rows over entire length of inner penial wall; apical portion of inner penial wall supporting a corrugated main pilaster and some additional shorter, rather indistinct, smooth longitudinal pilasters (Fig. 41).

Australocosmica Köhler, 2011

Australocosmica Köhler, 2011: 199–216. Type species: *Australocosmica augustae* Köhler, 2011, by original designation.

Diagnosis

Shell: Medium sized (D = 13–18 mm; Table 2), moderately thick, broadly conical to subglobose, moderately elevated; umbilicus narrowly winding. Protoconch with weak, radially elongated pustulation. Teleoconch sculptured by strongly developed radial ribs, ribs extent to periphery of whorl being replaced by fine growth lines on base of shell; whorls slowly increasing, separated by deep suture; periphery well rounded to slightly depressed. Shell colour uniform, yellowish brown to brownish-horn; periostracum glossy.

Radula: 3.0–5.5 mm long, with 120–150 rows of teeth, C + 12–14 + 3–4 + 13–16.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; inner penial wall sculpture consists marked of longitudinal pilasters, dense pustulation, or a combination of both; epiphallus lacking; penial retractor muscle attached to junction with vas deferens. Vas deferens entering penial sheath halfway up to almost apically, entering penial chamber through conspicuously thickened, furrowed, collar-like vergic papilla. Bursa copulatrix simple, short (slightly extending anterior end of spermoviduct).

TABLE 2. Shell dimensions of *Australocosmica* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens.

Species	N	Height (H)	Diameter (D)	Height of Last Whorl (LW)	Whorls	H/D Ratio
A. augustae	15	12.7–16.3 (14.5 ± 1.1)	15.3–18.2 (16.8 ± 0.8)	9.8–12.3 (11.1 ± 0.7)	4.7–5.2 (5.0 ± 0.2)	0.80–0.93 (0.86 ± 0.04)
A. sanctumpatriciusae						
Island	12	11.4–13.2 (12.3 ± 0.5)	15.0–16.4 (15.9 ± 0.5)	9.2–10.4 (9.6 ± 0.3)	3.9–4.7 (4.4 ± 0.2)	0.73–0.82 (0.77 ± 0.03)
Mainland	17	9.2–12.3 (11.0 ± 0.7)	14.6–17.8 (15.6 ± 0.9)	7.8–9.5 (8.8 ± 0.4)	4.2–4.6 (4.4 ± 0.1)	0.63–0.76 (0.71 ± 0.04)
A. vulcanica	32	9.4–11.5 (10.4 ± 0.6)	13.1–15.0 (13.8 ± 0.4)	7.6–9.0 (8.3 ± 0.3)	3.7–4.7 (4.3 ± 0.2)	0.69–0.81 (0.75 ± 0.03)
spec. A	6	12.9–14.6 (13.4 ± 0.6)	14.6–16.7 (15.3 ± 0.7)	9.7–11.0 (10.2 ± 0.5)	4.5–5.2 (4.7 ± 0.2)	0.81–0.95 (0.87 ± 0.04)
spec. B	2	14.0–14.8 (14.4 ± 0.4)	17.7–17.8 (17.8 ± 0.1)	11.2–11.7 (11.5 ± 0.3)	4.6–5.6 (5.1 ± 0.5)	0.79–0.84 (0.81 ± 0.02)

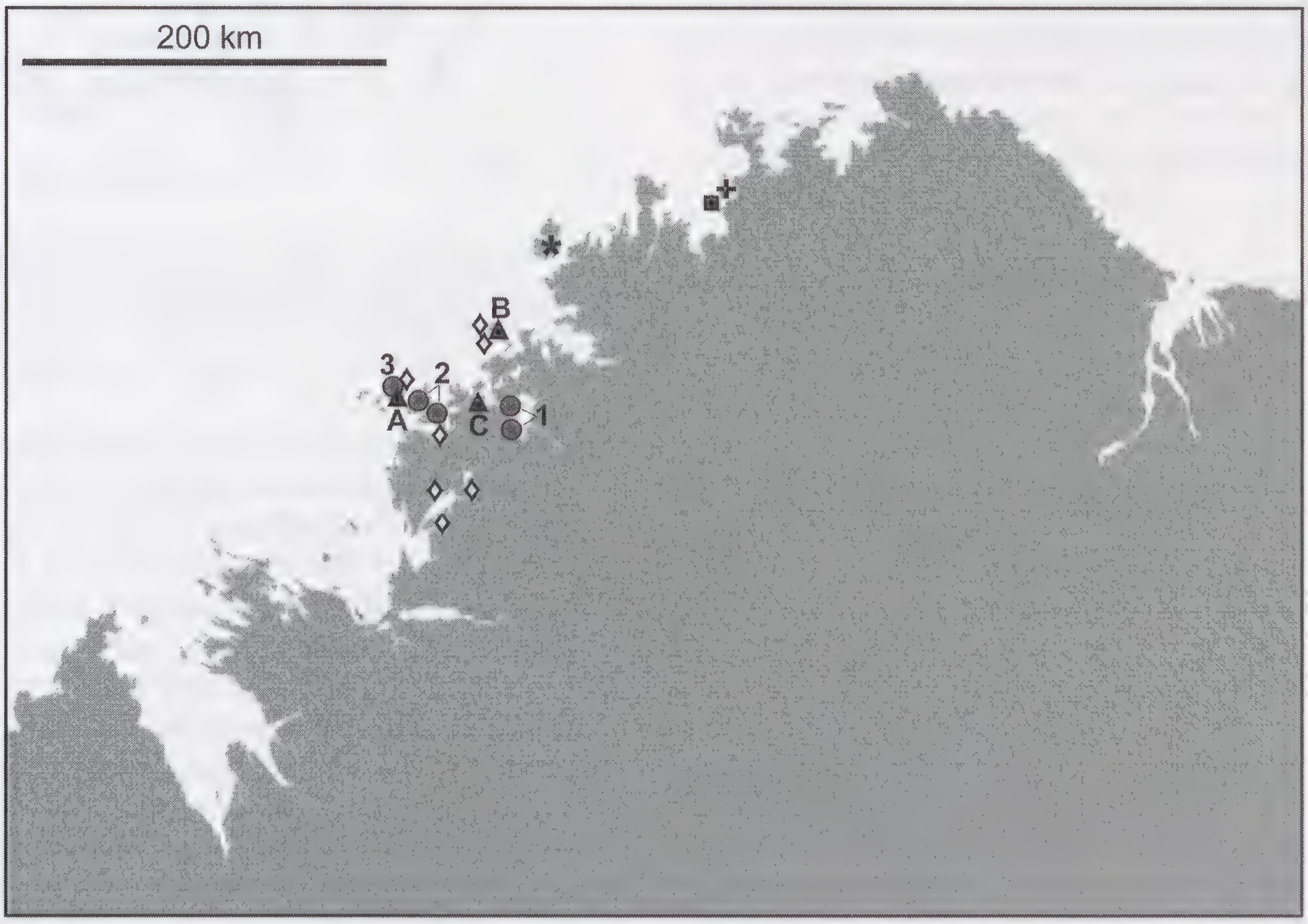

FIG. 42. Distribution map of *Carinotrachia*, *Kimberleymelon*, *Kimberleydiscus* and *Australocosmica*: + = *Carinotrachia admirale admirale* and *Kimberleymelon tealei* (Middle Osborn Island); ■ = *Carinotrachia admirale admirale* (Southwest Osborn Island); * = *Kimberleydiscus fasciatus* (Bigge Island); circles = records of *Australocosmica* species treated herein: 1: *A. sanctumpatriciusae* (St. Patrick Island and opposite mainland), 2: *A. augustae* (Augustus Island), 3: *A. vulcanica* (unnamed island in Vulcan Islands); triangles = records of undescribed species listed herein: A: *Australocosmica* spec. A (D'Arcy Island), B: *Australocosmica* spec. B (Coronation Island), C: *Australocosmica* spec. C (mainland, 1.3 km S of Halfway Bay); diamonds = records of undescribed *Australocosmica* species listed by Solem (1991).

Aestivation Strategy

Free sealer.

Diversity and Distribution (Fig. 42)

Currently known only from coastal portions of the mainland along the gulfs of St. George Basin and George Water, Prince Regent region, as well as from various islands in York and Camden sounds, Brunswick and Hanover bays. Next to three species described by Köhler (2011), seven additional, yet undescribed species were collected at various locations; material deposited with the Field Museum, Chicago (species 39, 40, 76–80 preliminarily identified by Alan Solem). In addition, three further undescribed species were collected during the Kimberley Island Survey but lack of preserved material prevented formal description: "spec. A" from D'Arcy Island, "spec. B" from Coronation Island, "spec. C" from mainland near Halfway Bay (Köhler, 2011). One undescribed species was collected on an unnamed island near the mouth of Sale River, Doubtful Bay, by Vince Kessner in 2010. Consequently, in addition to the three named species, there are probably at least 11 undescribed species.

Australocosmica augustae Köhler, 2011
Figs. 37H, 43

Australocosmica augustae Köhler, 2011: 204–206, figs. 2A, 3–5.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, NW section of Augustus Island, 15°20'11"S, 124°31'10"E (KIS 1–67).

Material Examined

Holotype WAM S34667 (preserved specimen, Fig. 37H). Paratypes WAM S37635 (10 preserved specimens), AM C465175 (5 preserved specimens). Additional, non-type material WAM S37633 (preserved juvenile), WAM S49023 (8 shells) from southern section, 15°23'52"S, 124°38'30"E; WAM S37634 (preserved specimen), AM C465176 (5 shells) from SE section, 15°23'45"S, 124°37'47"E.

Diagnosis

Shell: 13–16 mm in height, 15–18 mm in diameter (Table 2), thin (translucent) in juveniles, thick in adults; whorls slightly shouldered underneath suture; inner lip colour whitish; aperture with thinly callued parietal wall, forming an angle of 45° in adults, 30° in juveniles; outer lip thin, slightly expanded; protoconch ~ 3.5 mm in diameter with 1.5 whorls, with very fine, indistinct axial pustulation (Fig. 37H).

Genital anatomy: Penis straight, as long as anterior part of oviduct; penial retractor muscle longer than penis; inner penial wall smooth, three longitudinal pilasters forming along entire length of inner penial, two on each side of vergic ring, a third shorter, weaker underneath vergic opening (Fig. 43). Vagina moderately long, posteriorly inflated; inner wall with two or three smooth longitudinal pilasters.

Distribution and Ecology (Fig. 42)

Endemic to Augustus Island; found in vine thickets active on ground (leg. V. Kessner, 13.02.2009).

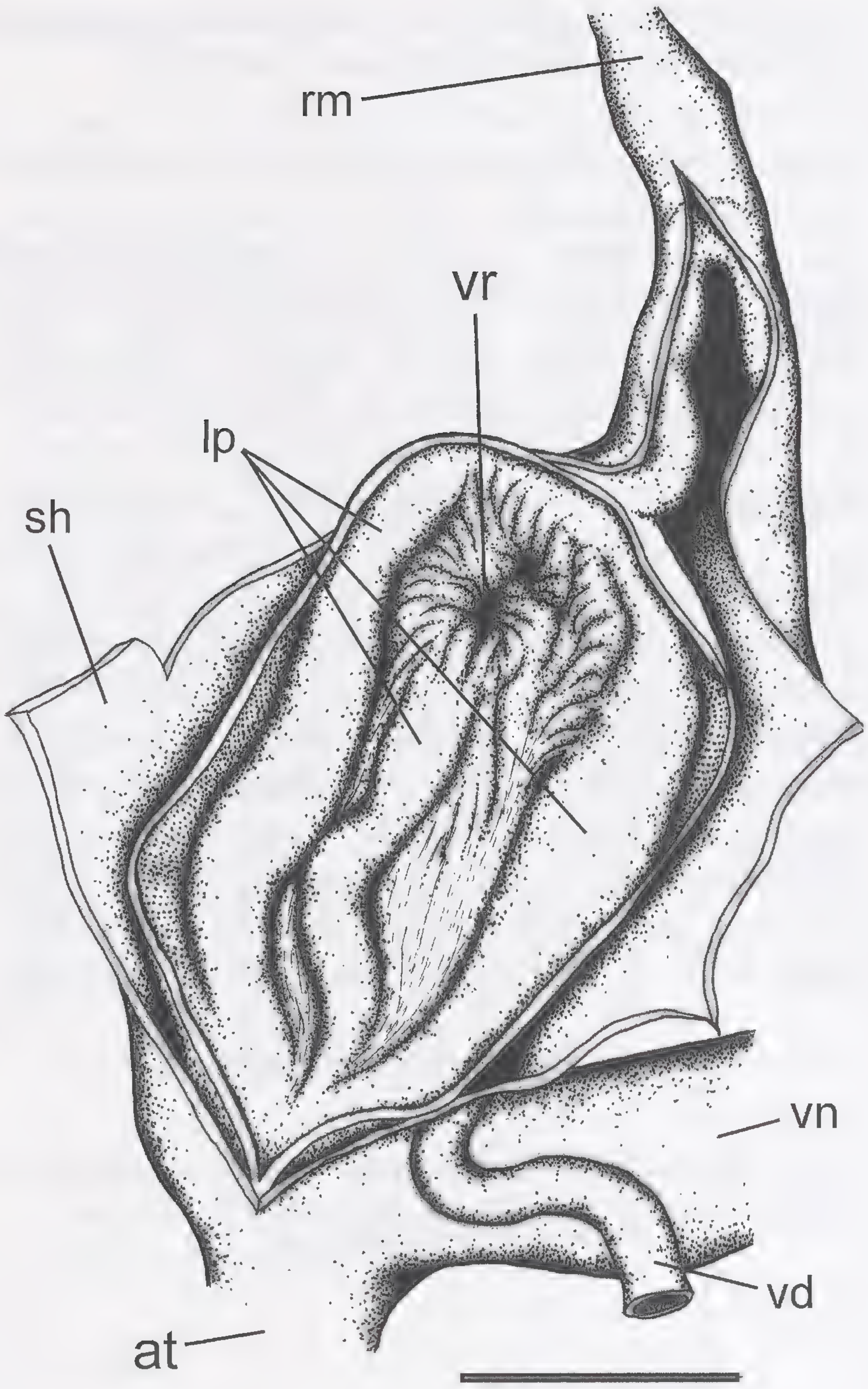

FIG. 43. Penial anatomy of *Australocosmica augustae* (AM C465175, Augustus Island, February). Scale bar = 1 mm.

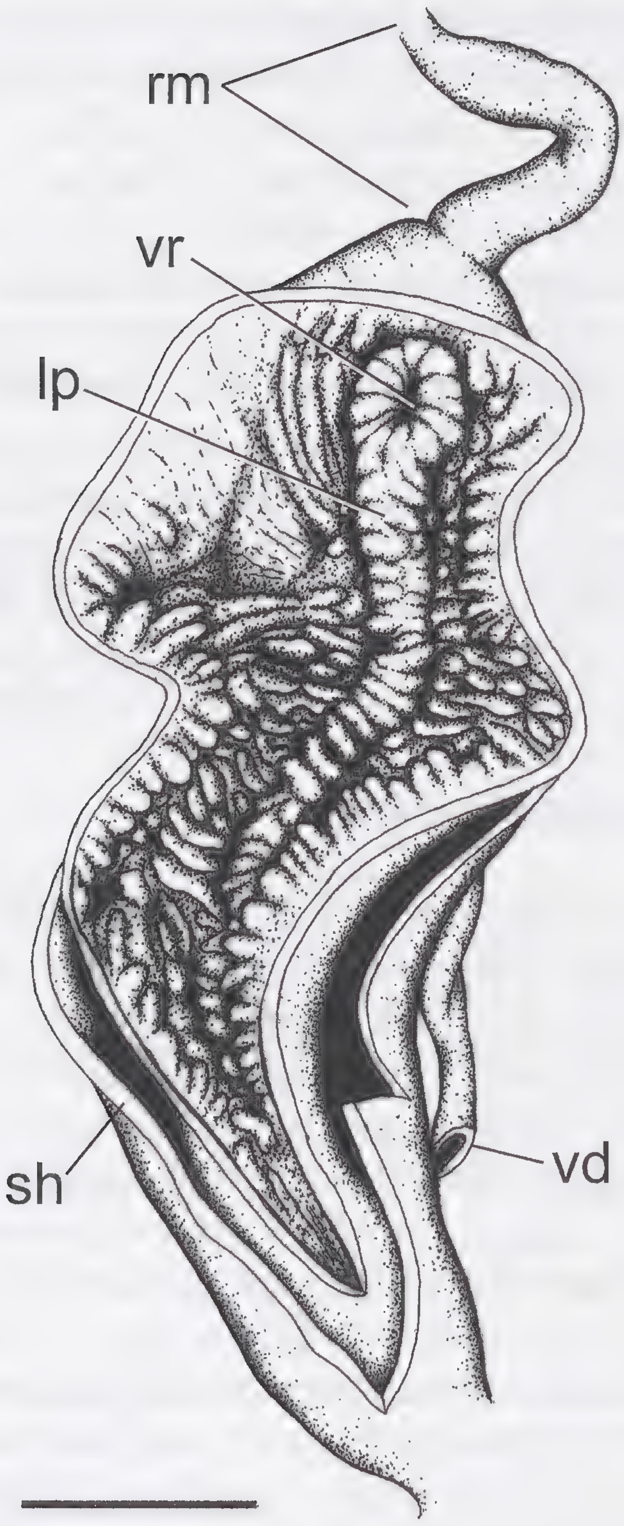

FIG. 44. Penial anatomy of *Australocosmica sanctumpatriciusae* (WAM S37637, St Patrick Island, February). Scale bar = 1 mm.

Australocosmica sanctumpatriciusae Köhler, 2011
Figs. 37I, 44

Australocosmica sanctumpatriciusae Köhler, 2011: 206–208, figs. 2B, C, 6–8.

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, St. Patrick Island, 15°21'23"S, 124°57'55"E (KIS 2–64).

Material Examined

Holotype WAM S37666 (preserved specimen, Fig. 37I). Paratypes WAM S37637 (2 preserved specimens), WAM S49021 (6 shells), AM C465173 (5 shells) from type locality.

Further, non-type material WAM S37638 (3 preserved specimens), WAM S49022 (13 shells), AM C465174 (5 shells) from small peninsula ca. 8 km SE of St. Patrick Island, 15°26'02"S, 125°00'23"E.

Diagnosis

Shell: 11–13 mm in height, 15–16 mm in diameter (Table 2), thin; whorls moderately wide in cross-section, slightly shouldered underneath suture, periphery well rounded to slightly angulated; teleoconchwith very thin, dense, regularly spaced radial ribs; inner lip whitish; with thinly callued parietal wall, angle of aperture 60°; outer lip thin, very slightly expanded; umbilicus forming chink; protoconch ~ 2.5 mm in diameter, ~ 1.5 whorls, with very fine, indistinct axial pustulation (Fig. 37I).

Genital anatomy: Penis as long as anterior part of oviduct, penial retractor muscle about as long as penis, proximal end of inner penial wall with obliquely arranged, fine, irregular transversal folds being distally replaced by rather large, rhomboid pustules that comprise most of wall; a well-developed, corrugated pilaster forms anteriorly of vergic opening (Fig. 44). Inner wall of vagina and anterior oviduct with many delicate longitudinal pilasters. Bursa copulatrix short.

Comparative Remarks

Shell shape and size are intermediate between *A. augustae* and *A. vulcanica*. Topotypic specimens with smaller and flatter shell than *A. augustae*, larger than *A. vulcanica*. In topotypic specimens umbilicus forms a chink like in *A. augustae* but unlike *A. vulcanica*. Dense pustulation of entire penial wall and presence of a corrugated pilaster underneath vergic opening being the most distinctive feature. Specimens from mainland with slightly smaller shells, narrowly winding umbilicus (like *A. vulcanica*), but similar penial morphology and genetically not well differentiated are considered to be conspecific.

Distribution and Ecology (Fig. 42)

Found on St. Patrick Island and adjacent mainland (small peninsula ca. 8 km SE of St. Patrick Island) in vine thickets, among sandstone boulders, under rocks and in loose soil.

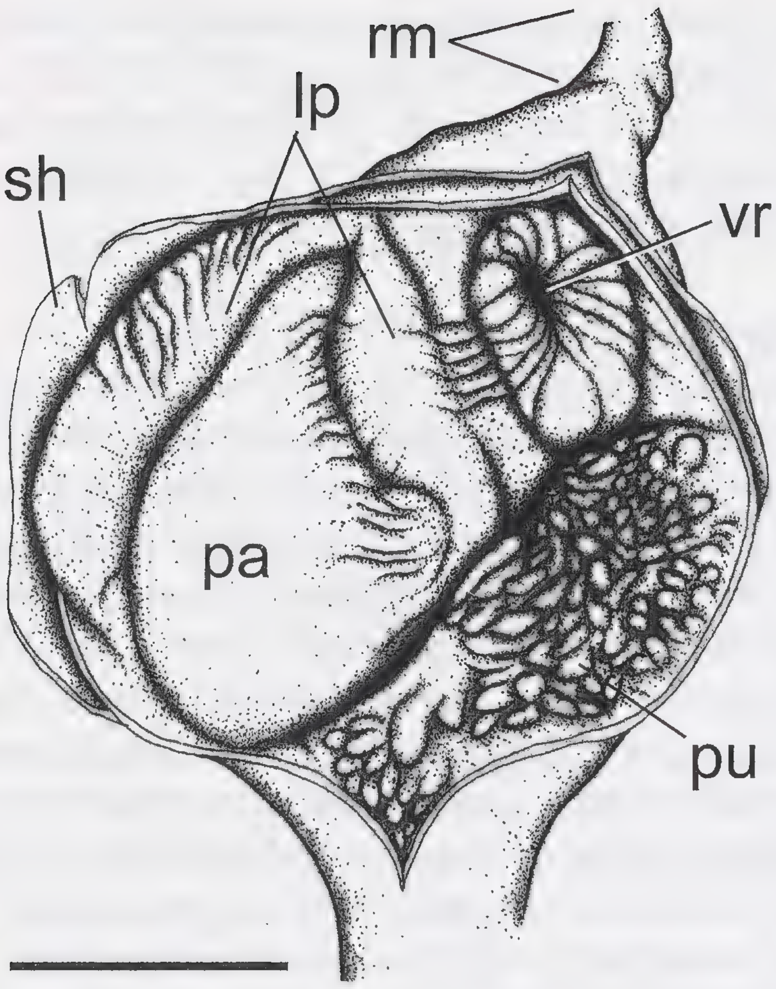

FIG. 45. Penial anatomy of *Australocosmica vulcanica* (AM C465177, unnamed island in Vulcan Islands group, February). Scale bar = 1 mm.

Australocosmica vulcanica Köhler, 2011
Figs. 37J, 45

Australocosmica vulcanica Köhler, 2011: 209–211, figs. 2D, 9–11.

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, unnamed island in Vulcan Islands, 1.4 km from NE corner of D'Arcy Island, 15°15'26"S, 124°24'22"E (KIS 2–63).

Material Examined

Holotype WAM S37668 (preserved specimen, Fig. 37J). Paratypes WAM S37636 (18 preserved specimens), AM C465177 (5 preserved specimens), WAM S49020 (13 shells), AM C465178 (10 shells) from type locality.

Description

Shell: Height 9–11 mm, diameter 13–15 mm (Table 2), thin; yellowish brown, inner lip whitish; whorls moderately wide in cross-section, well rounded to slightly angulated at periphery, slightly shouldered underneath suture; sculpture consists of very thin, dense, regularly spaced axial ribs; outer lip thin, very slightly expanded; umbilicus narrowly open or forming a chink; angle of aperture 60°; protoconch ~ 2.5 mm in diameter with ~ 1.5 whorls, with very fine, indistinct axial pustulation (Fig. 37J).

Genital anatomy: Penis strongly inflated, clearly shorter than anterior part of oviduct; penial retractor muscle about as long as penis; parts of inner penial wall pad-liked thickened, smooth, delimited by two thick, smooth longitudinal pilasters, distally with dense pustulation; pustules rather large, irregularly arranged (Fig. 45). Vagina moderately long, tubular; inner wall of vagina and anterior oviduct with two to three smooth longitudinal pilasters. Bursa copulatrix short.

Comparative Remarks

Shell smaller, flatter, with finer sculpture than *A. augustae* and smaller than *A. sanctumpatriciusae* (Table 2). Umbilicus narrowly winding instead of being entirely concealed as in *A. augustae*. Inflated penis proper and pad-like thickening of inner penial wall are diagnostic.

Distribution and Ecology (Fig. 42)

Only known from type locality where it is common in vine thickets on volcanic scree, in leaf litter and amongst boulders. Shells from D'Arcy Island appear to be larger and more elevated; their species identity remaining unclear (Köhler, 2011).

Kimboraga Iredale, 1939

Kimboraga Iredale, 1939: 47; Solem, 1985a: 818–846; 1991: 210–213; Solem & McKenzie, 1991: 247–263. Type species: *Chloritis micromphala* Gude, 1907, by original designation.

Taxonomic Remarks

The name *Kimboraga* was first used as *nomen nudum* by Iredale (1933, 1938) before being validly described by Iredale (1939); see Solem (1985a).

Diagnosis

Shell: Medium sized to large (D = 15–25 mm; Table 3), thin to moderately thick, conical to almost globose, moderately to strongly elevated; umbilicus narrowly winding, partly to almost completely concealed; protoconch rather smooth, with weakly developed radial growth lines, exceptionally with very weak radial pus-

TABLE 3. Shell parameters of *Kimboraga* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Height of Last Whorl (LW)	Whorls	H/D Ratio
K. glabra **n. sp.**	HT	13.9	21.6	10.3	4.0	0.64
	13	12.5–14.0 (13.2 ± 0.5)	19.5–21.8 (20.6 ± 0.7)	9.3–10.5 (9.9 ± 0.3)	3.8–4.2 (4.0 ± 0.1)	0.61–0.70 (0.64 ± 0.02)
K. exanima	12	14.3–18.3 (17.3 ± 1.1)	19.0–22.0 (21.0 ± 0.8)	10.8–13.2 (12.6 ± 0.6)	2.9–3.7 (3.3 ± 0.2)	0.75–0.91 (0.83 ± 0.04)
K. wulalam **n. sp.**	HT	18.5	23.7	13.3	3.9	0.78
	13	17.1–19.0 (18.2 ± 0.5)	22.4–24.3 (23.6 ± 0.5)	12.5–13.5 (13.0 ± 0.3)	3.7–4.2 (3.9 ± 0.1)	0.71–0.83 (0.77 ± 0.03)
K. cascadensis **n. sp.**	HT	17.2	22	13	3.8	0.78
	12	14.0–18.5 (16.4 ± 1.4)	19.2–24.0 (21.6 ± 1.5)	10.0–13.0 (11.8 ± 0.9)	3.5–4.1 (3.8 ± 0.2)	0.73–0.79 (0.76 ± 0.02)

tulation; teleoconch sculptured by very weak to well-developed, narrowly arranged radial ribs that continue onto the shell base; whorls rapidly increasing, separated by moderately deep to deep suture; periphery well rounded to slightly depressed. Shell colour more or less uniform, yellowish brown to brown, some species with reddish-purple suffusion, no colour banding.

Radula: ~ 3.0 mm long, C + 12–14 + 2–3 + 16–20.

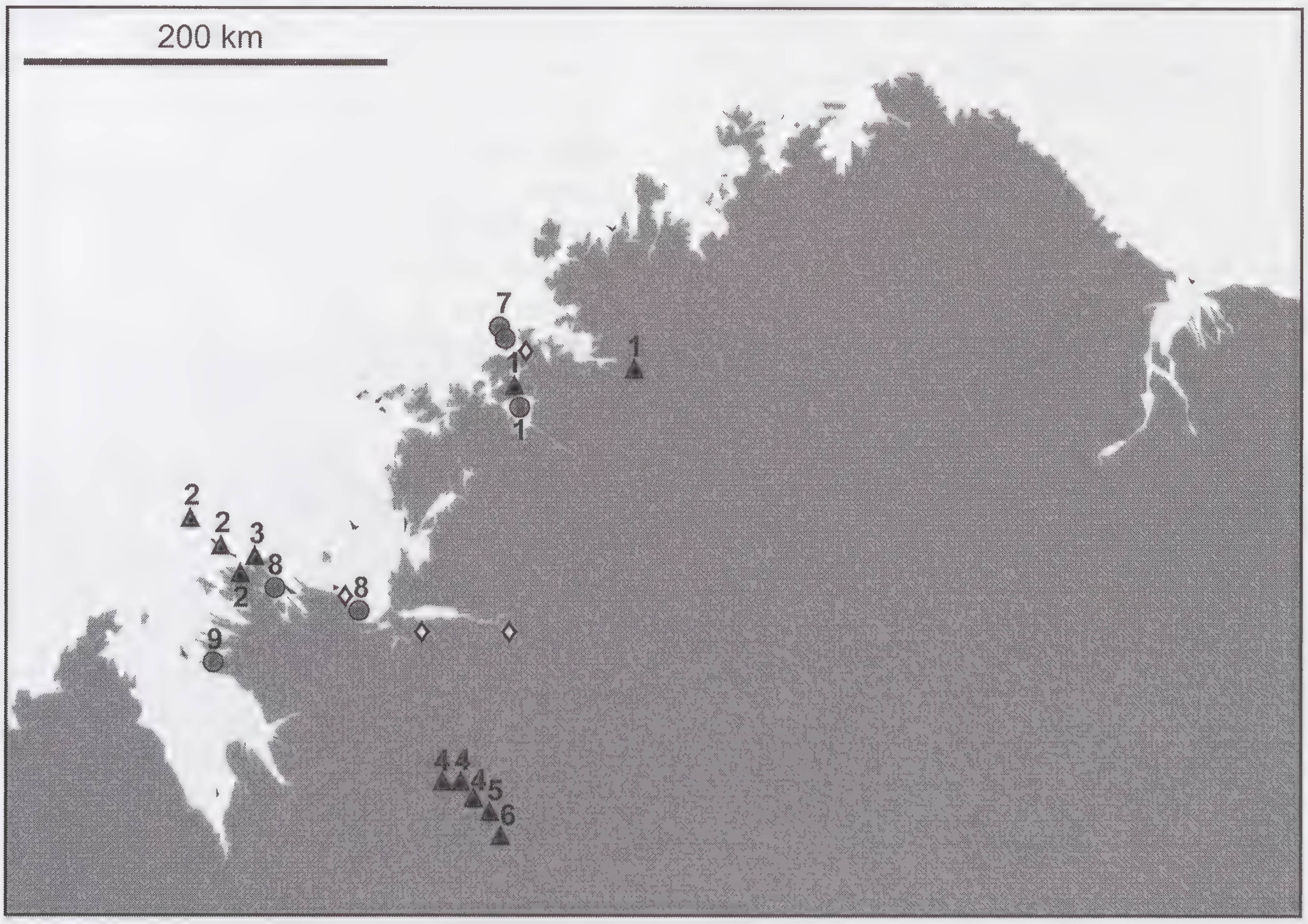

FIG. 46. Distribution map of *Kimboraga*. Circles = Records of species treated herein; triangles = species treated by Solem (1985, 1991); diamonds = records of undescribed taxa listed by Solem (1991): 1: *K. exanima*, 2: *K. yampiensis*, 3: *K. koolanensis*, 4: *K. mccorryi*, 5: *K. micromphalla*, 6: *K. yammerana*, 7: ***K. glabra*** n. sp., 8: ***K. wulalam*** n. sp., 9: ***K. cascadensis*** n. sp.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; inner penial wall sculpture consisting of rhomboid, relatively large pustules; epiphallus lacking; penial retractor muscle attached to junction with vas deferens. Vas deferens entering penial sheath in proximal third of penial complex, entering penial chamber through simple, vergic ring or cone-shaped verge. Bursa copulatrix simple varying in length, with inflated head, reaching or extending base of spermoviduct.

Aestivation Strategy

Rock sealer (modified after Solem, 1985a).

Diversity and Distribution (Fig. 46)

According to Solem (1985a), the genus currently contains six named species from Napier Ranges (three species), Prince Regent Reserve (one species), Yampi Sound (one or two species). In addition, Solem (1991) listed three undescribed species (NSP11, NSP12, NSP41) from SW Collier Bay and Walcott Inlet, as well as Cape Brewster. In the following four species are being newly described from Coronation, St. Patrick, Wulalam and Lachlan Islands.

Kimboraga glabra n. sp.

Figs. 37K, 47A, B

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, southern section of Coronation Island, 15°01’59”S, 124°57’15”E; coll. Vince Kessner, 2/06/2008, KIS 3–93 (vine thicket on upper SE-facing slopes, volcanic scree at base of cliffs and in crevices).

Material Examined

Holotype WAM S58437 (shell; Fig. 37K, Table 3). Paratypes AM C471723 (2 shells), WAM S37178 (4 shells) from type locality; WAM S37175 (shell) from 15°01’59”S, 124°56’53”E); WAM S37176 (9 shells) from 15°01’27”S, 124°56’28”E; WAM S37177 (shell) from 15°01’45”S, 124°56’49”E; AM C471724 (2 shells), WAM S49038 (2 shells) from 15°02’08.3”S, 124°57’06.1”E.

Etymology

From “*glaber*” (Latin, masculine = smooth), in reference to the characteristically smooth shell; adjective of feminine gender.

Description

Shell (Figs. 37K, 47A, B): Medium sized (D = 19.5–21.8 mm; Table 3), rather thin (translucent), broadly conical with low spire. Last whorl relatively narrow in cross-section, with well-rounded periphery, slightly depressed underneath well-incised suture. Umbilicus narrowly open, partly concealed. Protoconch with very weak radial pustulation. Teleoconch with very weak, narrowly arranged radial growth lines, most prominent on last whorl. Shell colour uniform, yellowish to reddish brown, with glossy surface. Aperture moderately wide, with simple, expanded lip, palatal or distal nodules absent, parietal wall inconspicuous.

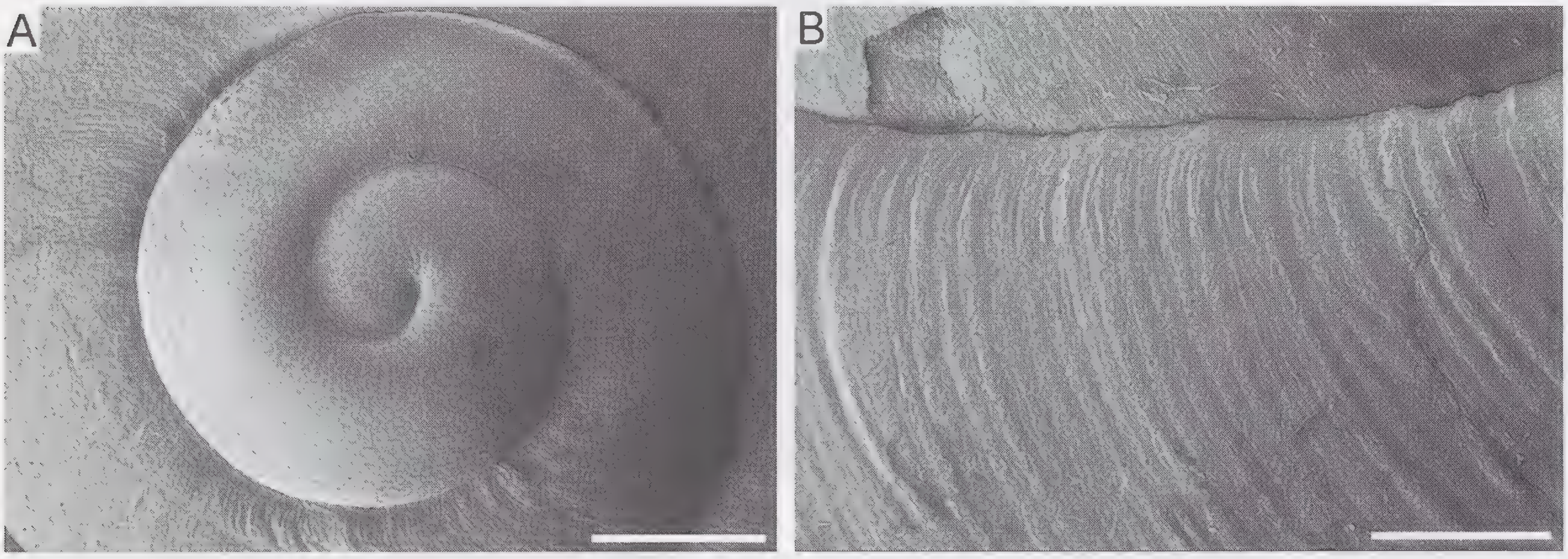

FIG. 47. SEM micrographs of the shell of ***Kimboraga glabra*** n. sp. paratype AM C471724 (Coronation island). A: Apical view showing protoconch; B: Details of sculpture on last whorl underneath suture. Scale bars = 1 mm.

Comparative Remarks

Known from dry shells only; differing from all other species by its broadly conical, low-spired shell, uninflated last whorl, glossy surface, absence of well-developed sculpture. It may well be identical with "*Kimboraga* NSP41" listed by Solem (1991), which was found on unnamed island in York Sound near Cape Brewster, immediately south of Coronation Island (RFS 12/2).

Distribution

Coronation Island, York Sound and possibly islands immediately south of Coronation Island.

Kimboraga exanima Solem, 1985

Figs. 37L, 48–50

Kimboraga exanimus [sic] Solem, 1985a: 835–836, figs. 205a–c.

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, Prince Regent River Reserve, below eastern face of Mt. Trafalgar, 15°17'S, 125°04'E.

Material Examined

From St. Andrews Island, George Basin: WAM S36695 (18 preserved specimens), AM C471725 (10 preserved specimens) from 15°21'24"S, 124°59'46"E; WAM S37621 (26 preserved specimens), AM C471726 (3 shells), WAM S49016 (5 shells), WAM S37415 (4 shells) from 15°21'22.7"S, 124°59'50"E; WAM S37622 (31 preserved specimens), AM C471727 (15 preserved specimens) from 15°21'29.5"S, 124°59'51.1"E; WAM S37605 (2 shells) from 15°21'26"S, 124°59'48"E.

Taxonomic Remarks

The species epithet "*exanimus*" (Latin = lifeless) introduced by Solem (1985) is an adjective. Because *Kimboraga* is of feminine gender, the correct name for this species is "*exanima*". Description based on dried shells from near Mt. Trafalgar; also reported from other mainland localities in NW Prince Regent Reserve (Solem, 1985a, 1991) (Fig. 46). Its anatomy has so far remained unknown. Material from St. Andrews Island, close to the type locality on opposite mainland, is preliminarily assigned to this species for a similar shell.

Description

Shell (Figs. 37L, 48A, B): Medium sized (D = 19–22 mm; Table 3), robust, conical with strongly elevated spire. Umbilicus almost completely concealed. Protoconch almost entirely smooth with very subtle radial growth lines. Teleoconch with well-developed, narrowly arranged radial growth lines, triangular in cross-section, evenly distributed across shell surface. Last whorl wide in cross-section, moderately

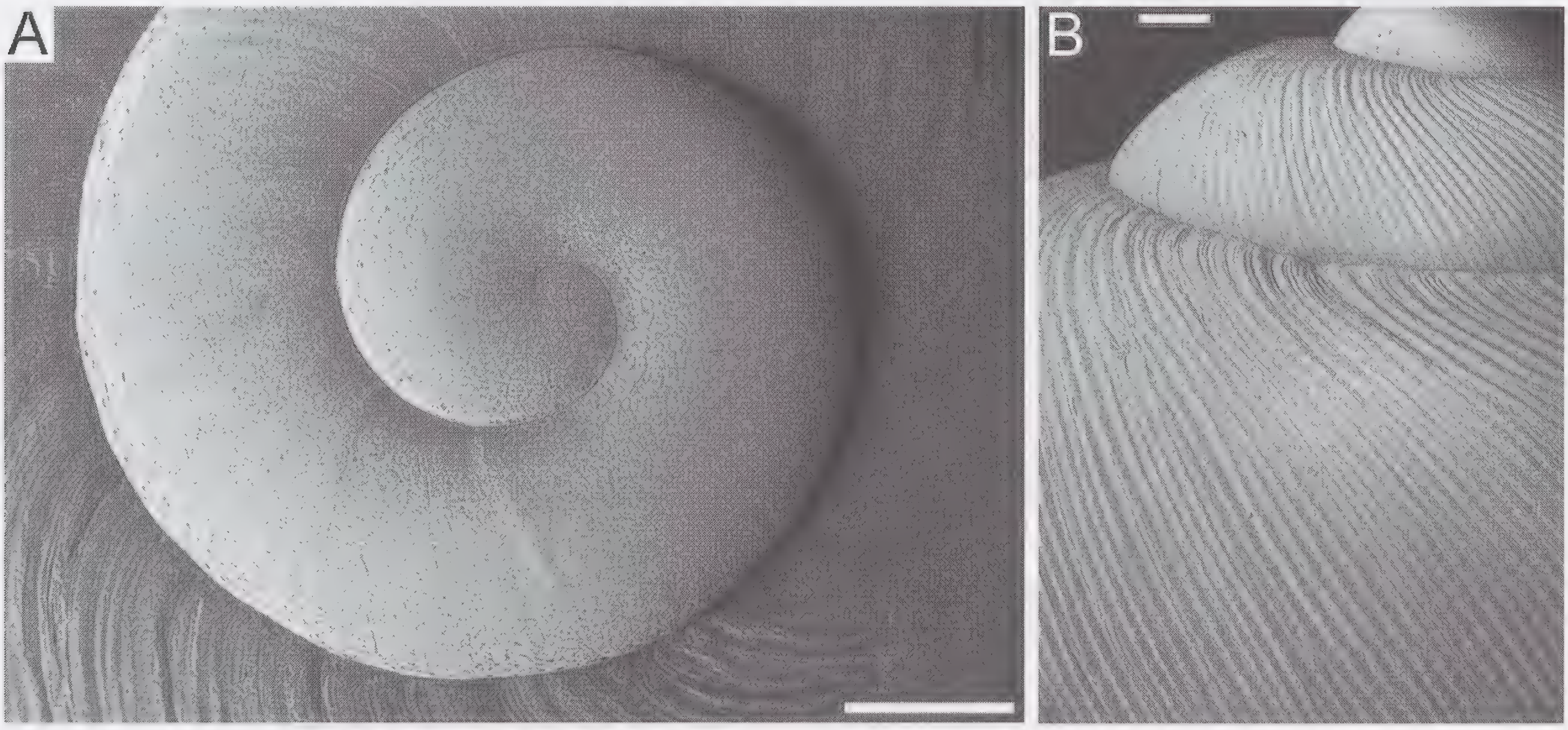

FIG. 48. SEM photographs of the shell of *Kimboraga exanima* AM C471726 (St Andrews Island). A: Apical view; B: Details of sculpture on first and second whorl. Scale bars = 1 mm.

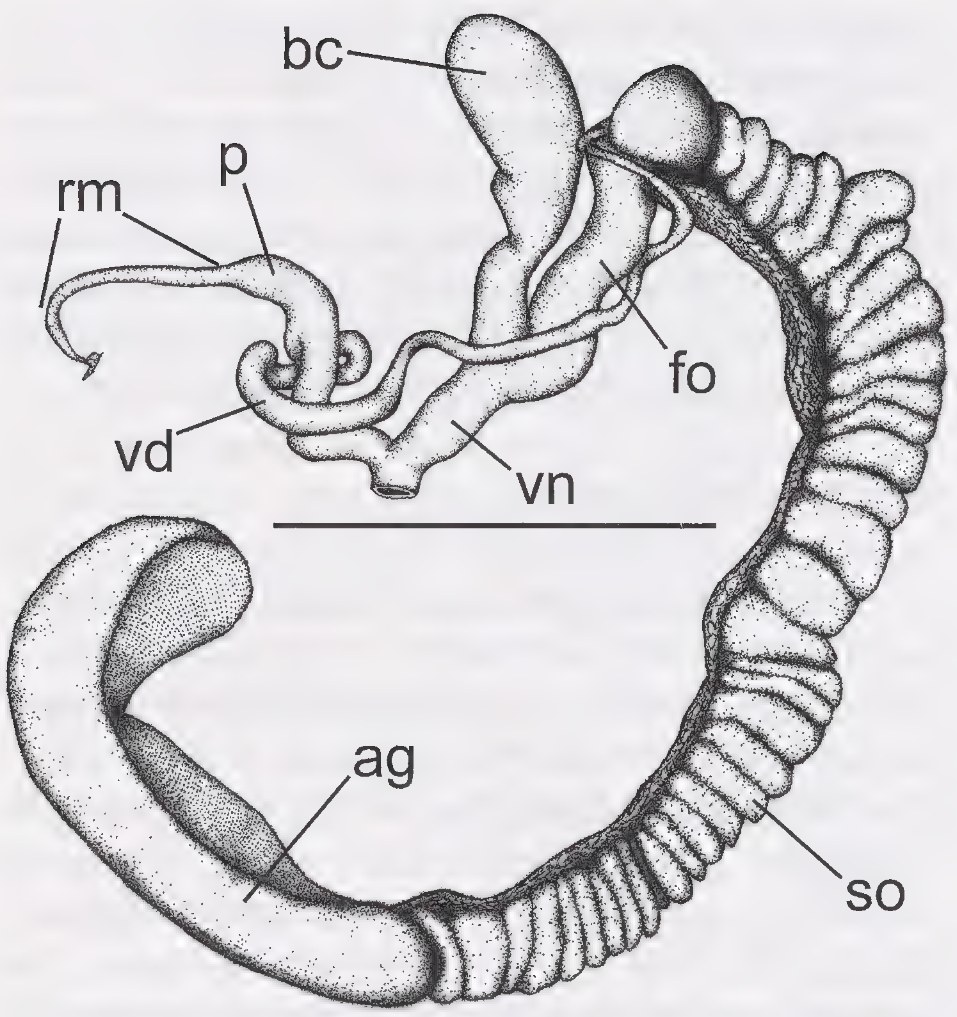

FIG. 49. Genital anatomy of *Kimboraga exanima* AM C471727 (St Andrews Island, May). Scale bar = 10 mm.

inflated, with well-rounded periphery, not depressed underneath well-incised suture. Shell colour blends from lighter yellowish brown at the tip to dark reddish brown on last whorl, base of shell brownish to yellowish horn, with glossy surface. Aperture wide, inside reddish brown with white outer margin, with simple, expanded lip, palatal or distal nodules absent, parietal wall slightly callued.

Genital anatomy (Figs. 49–50): Penis very small, very narrow, tubular (thinner than vas deferens!), coiled within thick penial sheath; penial complex about as long as vagina; penial retractor muscle same length as penial complex. Vas deferens comparatively thick. Inner penial wall supporting sparsely distributed, rhomboid pustules. Vagina moderately short. Bursa copulatrix short, reaching base of spermoviduct.

Comparative Remarks

Shells from St. Andrews Island differ from type specimens in larger size, slightly lower H/D ratio and lower whorl number. *Kimboraga exanima* differs from ***K. glabra*** by much stronger elevation (different H/D ratio), lower number of whorls, stronger sculpture, darker colour and more inflated last whorl (Table 3). Genitalia differ from all other species most conspicuously by narrowly tubular penis with sparse pustulation of inner penial wall.

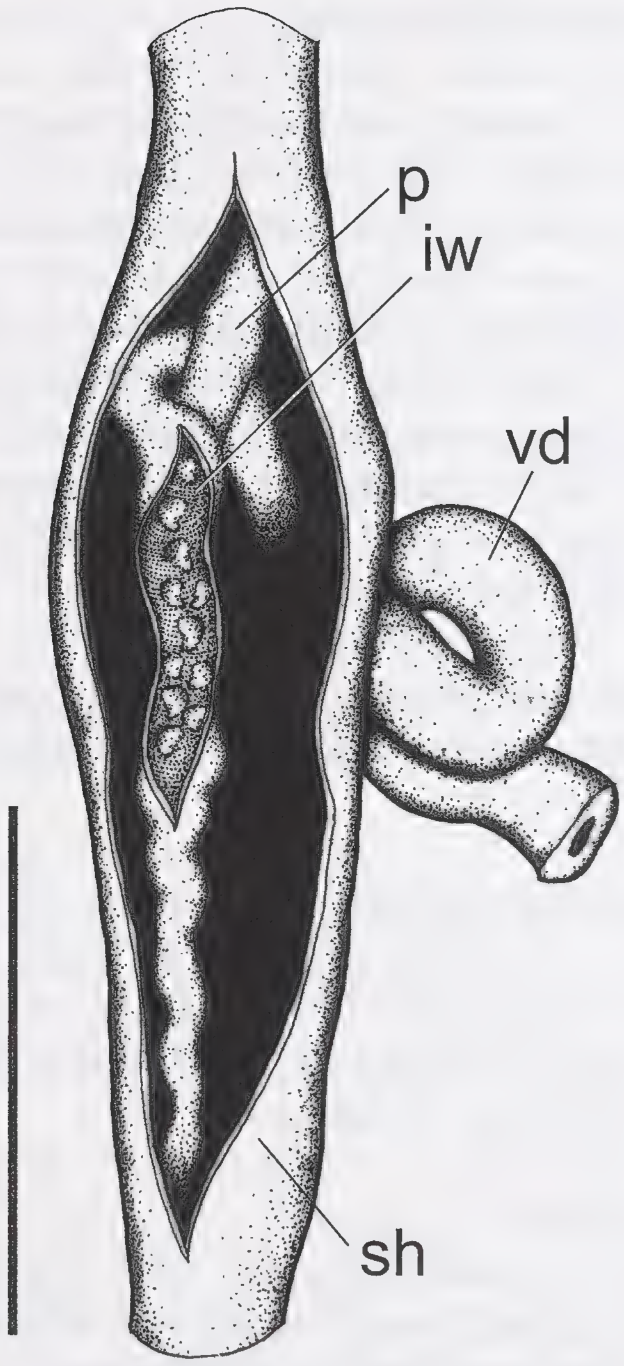

FIG. 50. Penial anatomy of *Kimboraga exanima* AM C471727 (St Andrews Island, May). Scale bar = 2 mm.

Distribution (Fig. 46)

Northwestern parts of Prince Regent Reserve and St. Andrews Island, Saint George Basin.

Kimboraga wulalam n. sp.
Figs. 37M, 51A–C, 52, 53

Type Locality

Western Australia, southwest Kimberley coast, Collier Bay, Wulalam Island, 16°22'13.4"S, 124°13'46.7"E; coll. Sean Stankowskii, 22/05/2009, KIS 2–73 (cliff face with scree, at base of creek line, in scree piles).

Material Examined

Holotype WAM S58438 (preserved specimen, Fig. 37M, Table 3). Paratypes WAM S37731 (20 preserved specimens), AM C471728 (10 preserved specimens), WAM S37824 (4 shells) from type locality; WAM S37732 (preserved specimen) from 16°21'56.8"S, 124°13'45.7"E; WAM S37733 (6 preserved specimens) from 16°22'18"S, 124°14'05"E; WAM S37793 (6 preserved specimens), WAM S37823 (3 shells) from 16°22'24.6"S, 124°13'52.5"E; WAM S49244 (11 preserved specimens) from 16°22'15.6"S, 124°13'45.3"E.

Additional non-type material. WAM S49245 (59 preserved specimens), AM C471729 (20 preserved specimens) from small, unnamed island N of Wulalam Island, 16°20'33"S, 124°13'36"E; WAM S49246 (108 preserved specimens), AM C471730 (70 preserved specimens) from small island E of Molema Island, Talbot Bay, 16°14'04"S, 123°50'36"E.

Etymology

For Wulalam Island, noun in apposition.

Description

Shell (Figs. 37M, 51A–C): Medium sized (D = 22–25 mm, Table 3), robust, conical with moderately elevated spire. Umbilicus almost completely concealed. Protoconch with very subtle radial growth lines. Teleoconch with well-developed, narrowly arranged radial growth lines, triangular in cross-section, evenly distributed across shell surface. Last whorl wide in cross-section, moderately inflated, with well-rounded periphery, not depressed underneath well-incised suture. Shell colour blends from lighter yellowish brown at tip to dark reddish brown on last whorl, base of shell brownish to yellowish horn, with glossy surface. Aperture wide, inside whitish, with simple, slightly expanded lip, palatal or distal nodules absent, parietal wall inconspicuous.

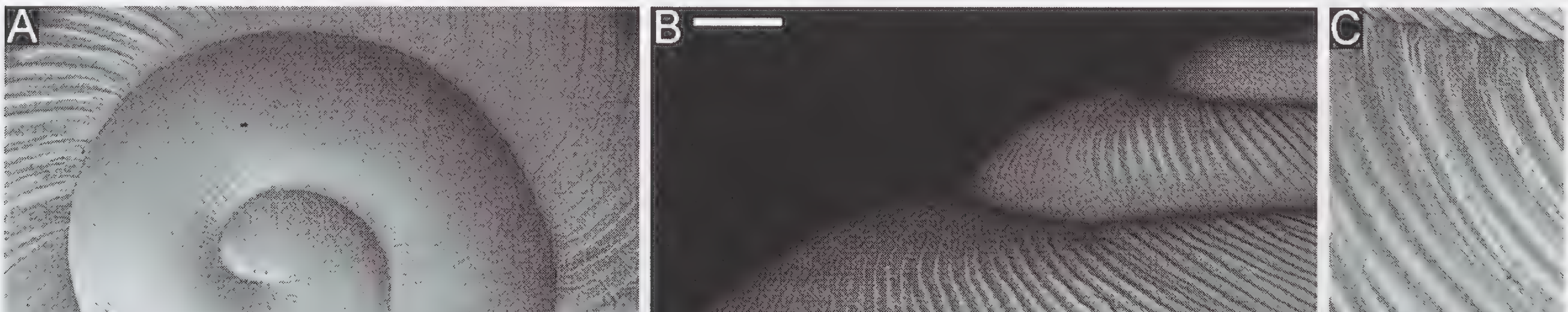

FIG. 51. SEM micrographs of ***Kimboraga wulalam*** n. sp. (Wulalam Island). A–C: Shell, paratype AM C471728. A: Apical view showing protoconch; B: Lateral view showing sculpture on first to third whorl; C: Detail of sculpture on first whorl. Scale bars A–B = 1 mm, C = 0.5 mm. D: Jaw, paratype WAM S37793. Scale bar = 0.5 mm. E–F: Radula, paratype WAM S37793; E: Central and inner lateral teeth viewed from above; F: Close-up of inner to middle marginal teeth. Scale bars = 100 µm.

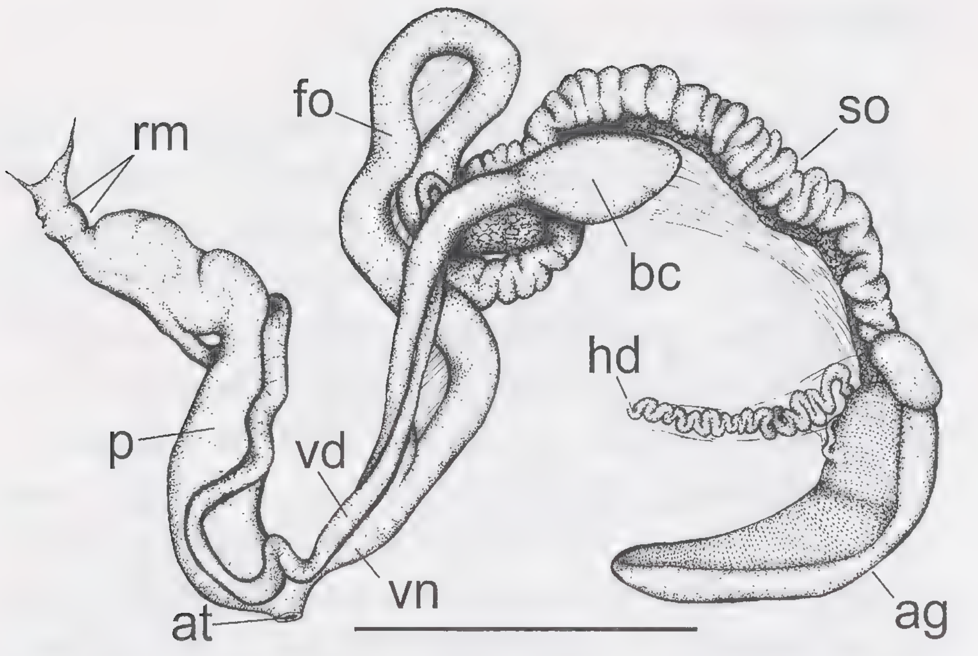

FIG. 52. Genital anatomy of ***Kimboraga wulalam*** n. sp. paratype AM C471728 (Wulalam Island, May). Scale bar = 10 mm.

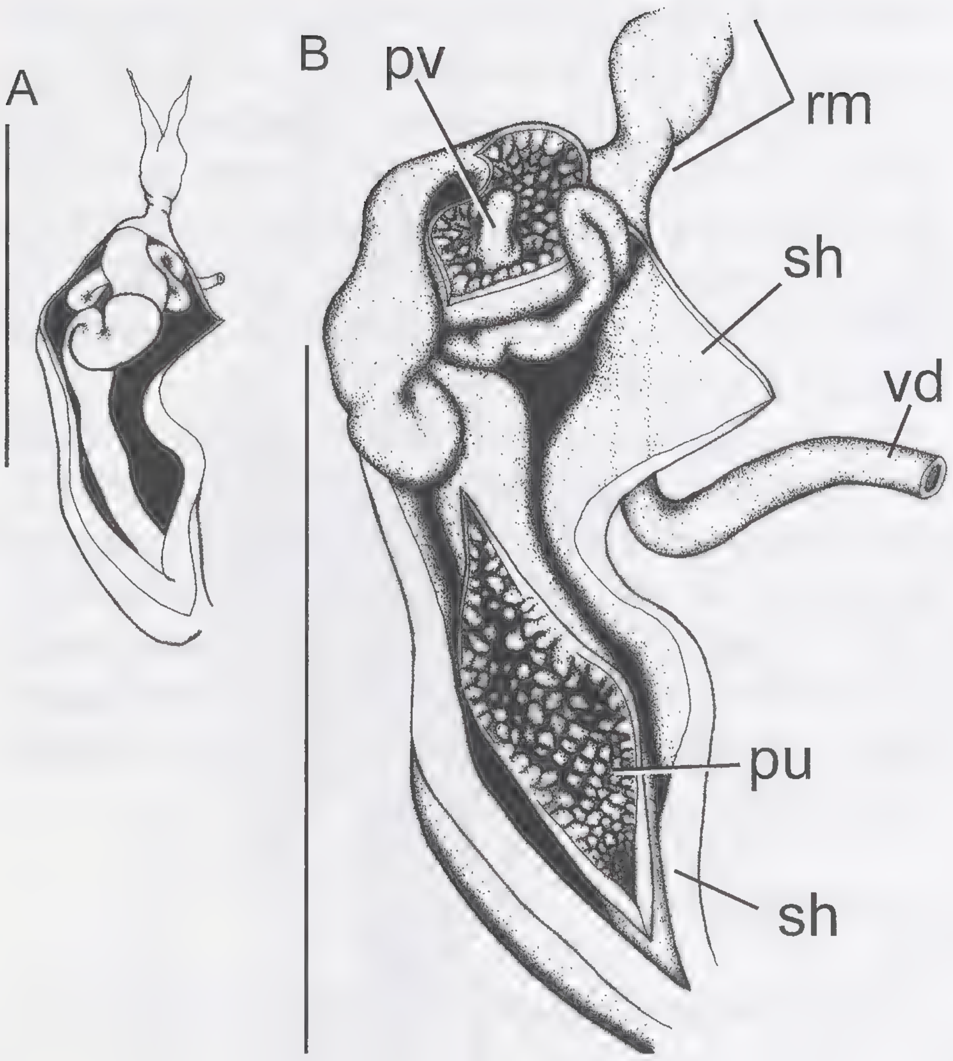

FIG. 53. Penial anatomy of ***Kimboraga wulalam*** n. sp. paratype AM C471728 (Wulalam Island, May). A: Schematic overview showing penis coiled in penial sheath; B: Detail showing interior of penial wall at distal and proximal end of penis. Scale bars = 10 mm.

Digestive anatomy: Jaw with 11 regular plates (Fig. 51D). Radula 5.5 mm long with 120–170 rows of teeth; C + 10 + 4 + 16 (Fig. 51E–F).

Genital anatomy (Figs. 52–53): Penis moderate in size, narrowly tubular (thicker than vas deferens), coiled within thick penial sheath; penial complex about as long as vagina; penial retractor muscle stubby. Vas deferens comparatively thick, entering sheath near apex of penial complex, entering lumen of penial chamber through a tubular verge. Inner penial wall supporting densely packed, rhomboid pustules over entire length. Vagina rather short. Bursa copulatrix moderately long, extending base of spermoviduct.

Comparative Remarks

Shell differs from ***K. glabra*** by stronger elevation, stronger sculpture and more inflated last whorl; from *K. exanima* by larger size, more whorls, less elevated spire and white colour of inner lip (Table 3). Genitalia differ from other species most conspicuously by presence of well-developed penial verge, from *K. exanima* by thicker size of penis and stronger pustulation of penial wall.

Distribution (Fig. 46)

Wulalam Island in Collier Bay and Molema Island plus unnamed island in Talbot Bay.

Kimboraga cascadensis n. sp.

Figs. 37N, 54C–D, 55, 56

Type Locality

Western Australia, southwest Kimberley coast, Buccaneer Archipelago, King Sound, Lachlan Island, 16°37'20.6"S, 123°28'15.7"E; coll. Frank Köhler, 25/05/2009, KIS 1–71 (E-facing base of sandstone cliffs, under rocks).

Material Examined

Holotype WAM S58439 (preserved specimen; Fig. 37N, Table 3). Paratypes WAM S37730 (2 preserved specimens, dissected), WAM S37821 (3 shells) from type locality; WAM S37792 (preserved specimen), WAM S37822 (2 shells) from 16°37'20.7"S,123°28'05.6"E; WAM S37820 (3 shells) from 16°37'22.8"S, 123°28'06.4"E; WAM S49241 (8 preserved specimens) from 16°37'01.3"S, 123°29'21.6"E; WAM S49242 (8 preserved specimens) from 16°36'59.9"S, 123°28'35.1"E; WAM S49243 (13 preserved specimens), AM C471731 (5 preserved specimens) from 16°37'00.9"S, 123°28'18.4"E.

Additional non-type material WAM S49240 (5 preserved specimens) from unnamed island N of Lachlan Is., 16°36'10"S, 123°29'18"E.

Etymology

For Cascade Bay; adjective of feminine gender.

Description

Shell (Figs. 37N, 54A, B): Medium sized (D = 19–24 mm, Table 3), robust, conical with moderately elevated spire. Umbilicus almost completely concealed. Protoconch with very subtle radial growth lines. Teleoconch with well-developed, narrowly arranged radial growth lines, triangular in cross-section, evenly distributed across shell surface. Last whorl wide in cross-section, moderately inflated, with well-rounded periphery, not depressed underneath well-incised suture. Shell colour blends from lighter yellowish brown at tip to dark reddish brown on last whorl, base of shell brownish to yellowish horn, with glossy surface. Aperture wide, inside whitish, with simple, conspicuously expanded lip, palatal or distal nodules absent, parietal wall inconspicuous.

Radula (Fig. 54C–D): C + 10 + 4 + 14.

Genital anatomy (Figs. 55–56): Penis moderate in size, coiled within penial sheath, longer than vagina; penial retractor muscle short. Vas deferens comparatively thick, entering sheath near apex of penial complex. Inner penial wall entirely covered by densely arranged, rhomboid, large pustules, with longitudinal pilasters at distal end of inner penial. Vagina moderately long. Bursa copulatrix short, reaching base of spermoviduct.

Comparative Remarks

Shells from type locality, Lachlan Island, are smaller than those from an unnamed island north of it (D = 19.2–22.0 mm vs. 22.6–24 mm) but have similar proportions. Both are considered conspecific for close similarity. Shell is similar to ***K. wulalam*** but has a more conspicuously expanded lip. Genitalia differ from *K. exanima* and ***K. wulalam*** most conspicuously by larger and thicker penis with much denser pustulation, pustules larger. Inner penial wall pustulation similar to *K. yampiensis* Solem,

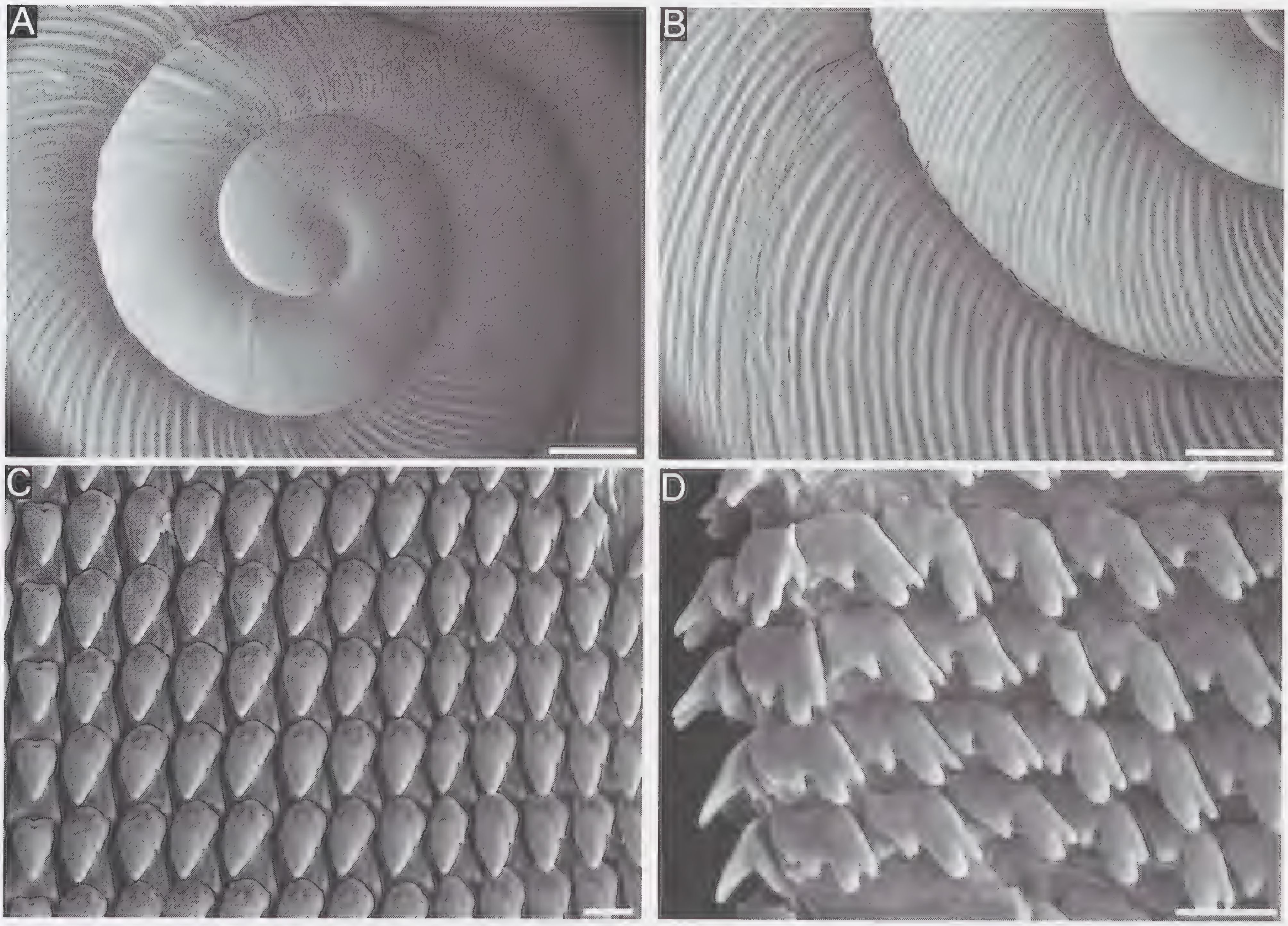

FIG. 54. SEM micrographs of ***Kimboraga cascadensis*** n. sp. paratype WAM S37730 (Lachlan Island). A–B: Shell. A: Apical view; B: Sculpture on first and second whorl. Scale bars = 1 mm; C–D: Radula. C: Central and inner lateral teeth viewed from above; D: Close-up of inner to middle marginal teeth. Scale bars = 100 μm.

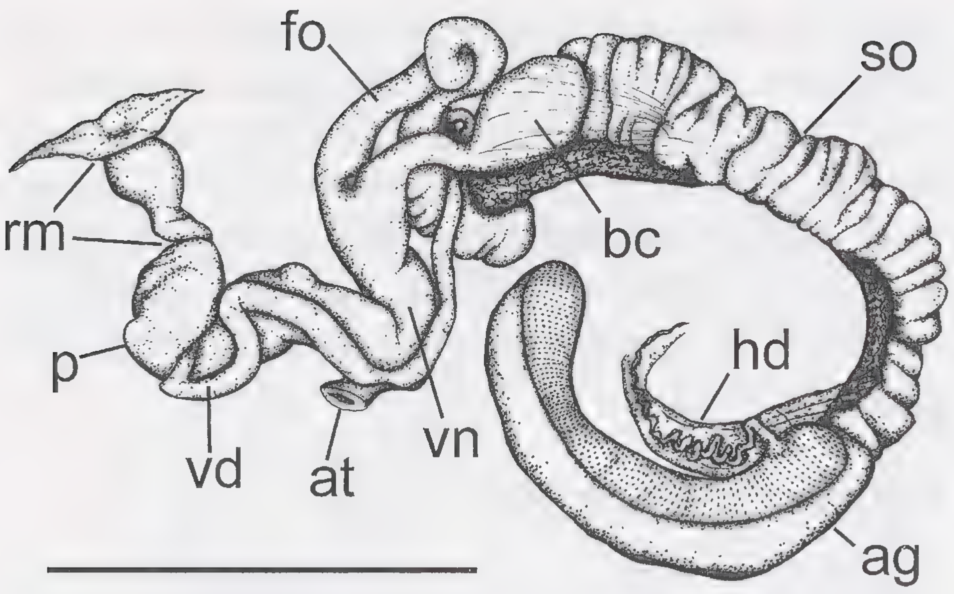

FIG. 55. Genital anatomy of ***Kimboraga cascadensis*** n. sp. paratype WAM S49242 (Lachlan Island, February). Scale bar = 10 mm.

1985, and *K. mccorryi* Solem, 1985. However, in *K. yampiensis* pustules are much smaller except for those that form a main pilaster; in both species longitudinal pilasters comprise distal half of inner penial wall, being much longer than in ***K. cascadensis***.

Distribution (Fig. 46)

Lachlan Island and an unnamed island N of Lachlan Island, Cascade Bay, King Sound.

Xanthomelon Martens, 1860

Xanthomelon Martens, 1860 [in Martens & Albers]: 174; Solem, 1979: 9–45 (partim); 1985a: 920–922 (partim); 1991: 175–178 (partim); Solem & McKenzie, 1991: 247–263 (partim). Type species: *Helix pomum* Pfeiffer, 1842 (= *Helyx durvillii* Hombron & Jacquinot, 1841), by original designation.

Taxonomic Remarks

The taxonomy of *Xanthomelon* is complicated. The generic name was introduced for the nominal species-taxon *Helix pomum* Pfeiffer, 1842, for its peculiarly globose, yellowish shell. The type locality was originally given as “Nova Seelandia?” but later corrected to “Port Essington in Neu-Holland” [Port Essington, Coburg Peninsula, 11°12”S, 132°09’E].

Solem (1979) considered *H. pomum* to be a junior synonym of *Helyx durvillii* Hombron & Jacquinot, 1841, from “Raffles Bay, Australia” [Raffles Bay, Coburg Peninsula, 11°12’S, 132°24”E]. Both type localities are indeed in very close proximity in the northeastern part of the Coburg Peninsula, Northern Territory.

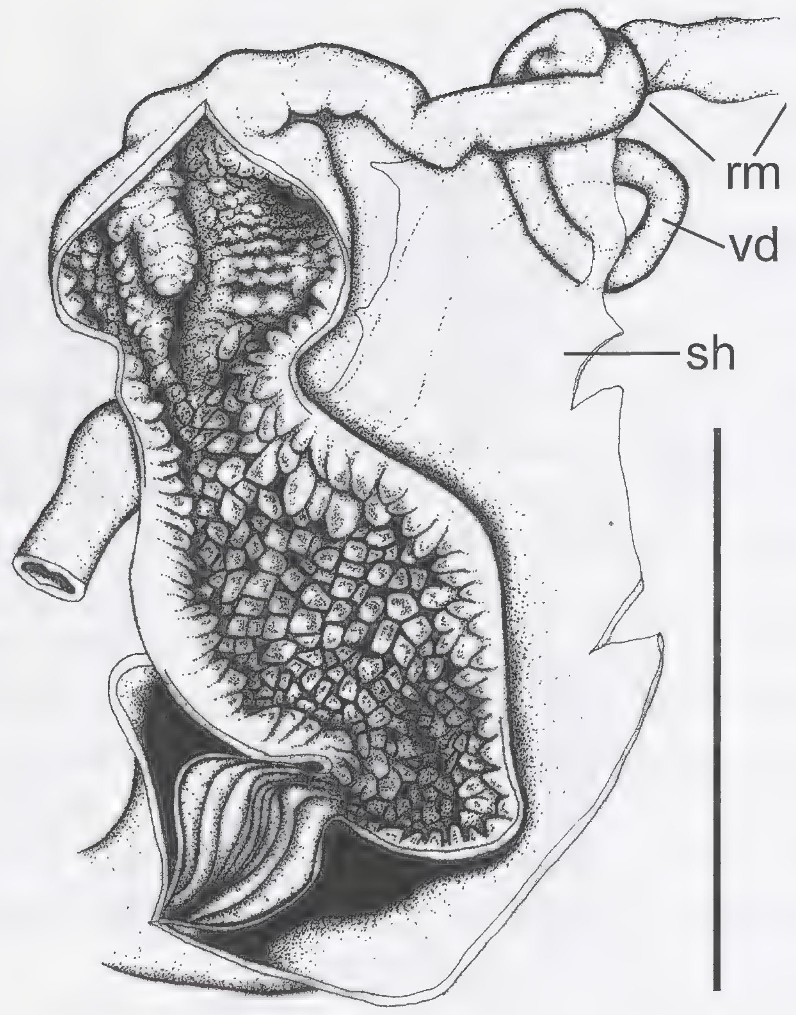

FIG. 56. Penial anatomy of ***Kimboraga cascadensis*** n. sp. paratype WAM S49242 (Lachlan Island, February). Scale bar = 5 mm.

Therefore, the suggested treatment of both nominal taxa as synonymous appears to be a plausible taxonomic solution given that currently there is no indication that Coburg Peninsula is inhabited by more than one species of *Xanthomelon*. Solem (1979) provided a comprehensive synonymy of *Xanthomelon durvillii*.

Based on a similar shell, Solem (1979) considered *Helix* (*Hadra*) *prudhoensis* E. A. Smith, 1894, to be congeneric. Because *H. prudhoensis* is the type species of *Globorhagada* Iredale, 1939, this genus-group taxon has since been treated as a junior synonym of *Xanthomelon*. Solem (1979) stressed that the name *Globorhagada* was arbitrarily employed to contain species with rounded shells, most of which belong to a number of different genera. However, a mitochondrial phylogeny of the Western Australian Camaenidae indicates that *H. prudhoensis* represents a monophyletic clade distinct from *Xanthomelon* (Köhler, 2009, 2010c). Therefore, the name *Globorhagada* is here removed from the synonymy of *Xanthomelon* and treated as a valid genus. Conversely, the genus *Xanthomelon* is restricted to species that are closely related to the type species *X. durvillii*, such as *X. obliquirugosa*. Stanisic et al. (2010) stated that *Xanthomelon* might be polyphyletic as based on microsculptures.

TABLE 4. Shell parameters of *Xanthomelon* and *Globorhagada*. Given are maximum – minimum (mean ± standard deviation) of shells for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Height of Last Whorl (LW)	Umbilicus (U)	No. of Whorls	H/D Ratio
X. obliquirugosa	20	18.0–25.9 (22.4 ± 1.8)	20.3–27.8 (24.2 ± 1.9)	13.4–18.1 (15.6 ± 1.3)	chink - 2.7	3.7–4.5 (4.3 ± 0.2)	0.84–1.02 (0.93 ± 0.04)
G. prudhoensis	14	28.8–35.1 (30.4 ± 1.5)	26.6–31.0 (29.1 ± 1.2)	19.2–21.0 (20.0 ± 0.5)	chink - 4.0	4.0–4.7 (4.2 ± 0.2)	0.93–1.16 (1.05 ± 0.06)
G. confusa n. sp.	HT	35.9	33.6	23.7	chink	4.6	1.07
	3	32.5–37.0 (35.1 ± 1.9)	31.6–34.8 (33.3 ± 1.3)	21.0–23.7 (22.3 ± 1.1)	chink - narrow	4.5–4.8 (5.1 ± 0.1)	0.93–1.17 (1.06 ± 0.10)
G. wurroolgu n. sp.	HT	26.5	28.8	20.6	chink	3.7	0.92
	8	25.3–29.0 (27.1 ± 1.0)	25.7–29.0 (27.3 ± 1.2)	17.8–20.6 (19.0 ± 0.9)	chink - narrow	3.7–4.5 (4.7 ± 0.2)	0.92–1.05 (0.99 ± 0.04)
G. yoowadan n. sp.	HT	31.5	30	21	chink	4.2	1.05
	8	27.4–35.5 (30.5 ± 2.5)	27.3–30.7 (28.9 ± 1.2)	18.3–22.6 (20.0 ± 1.4)	chink - narrow	4.1–4.5 (4.8 ± 0.1)	0.99–1.18 (1.05 ± 0.06)
G. wunandarra n. sp.	11	23.5–25.6 (24.5 ± 0.7)	20.6–22.3 (21.6 ± 0.5)	14.6–16.3 (15.4 ± 0.5)	chink - narrow	4.3–4.5 (4.8 ± 0.1)	1.06–1.18 (1.13 ± 0.03)
G. uwinsensis n. sp.	9	16.4–22.5 (19.7 ± 1.7)	16.1–20.0 (18.3 ± 1.2)	10.5–14.0 (12.6 ± 1.0)	narrow	4.0–4.3 (4.6 ± 0.1)	1.02–1.15 (1.08 ± 0.04)

Diagnosis

Shell: Large to very large (D >20 mm; Table 4), moderately thick, globose, strongly elevated with H/D ratio averaging 1.0; umbilicus narrowly open, partly concealed; protoconch with smooth or faintly pustulose sculpture; teleoconch with variable sculpture, with oblique (microscopic) radial corrugations; body whorl strongly enlarged, descending slightly but abruptly behind apertural lip; whorls rapidly increasing, separated by shallow suture; periphery well rounded to slightly depressed; aperture wide, columellar margin and parietal wall weakly to strongly callued. Shell colour more or less uniform, yellowish brown, no colour banding.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; penis coiled within sheath, inner penial wall entirely covered by pustulation (can be very fine); epiphallus lacking; penial retractor muscle attached to junction with vas deferens. Vas deferens entering penial sheath distally through simple vergic ring (pore). Bursa copulatrix simple, with globular head, reaching or extending base of spermoviduct.

Aestivation Strategy

Free sealer.

Comparative Remarks

A large number of nominal species taxa with uncertain systematic status were subsumed under the generic name *Xanthomelon*. These species have in common the conspicuous shell shape and size being generally considered as characteristic. As the systematic status of many nominal taxa remains uncertain, the comparison between *Xanthomelon* and *Globorhagada* is based on the four species described by Solem (1979): *X. durvillii*, *X. obliquirugosa*, *Globorhagada prudhoensis* and *G. ruberpumilio*. The shell of *Globorhagada* differs subtly by presence of an axial microsculpture of growth lines and/or rows of tiny pustules instead of oblique radial corrugations. *Xanthomelon durvillii* and *X. obliquirugosa* have a more globose shell with less elevated spire than *G. prudhoensis*. However, the shell of *G. ruberpumilio* is of the globose type known from *Xanthomelon*. The different structure of

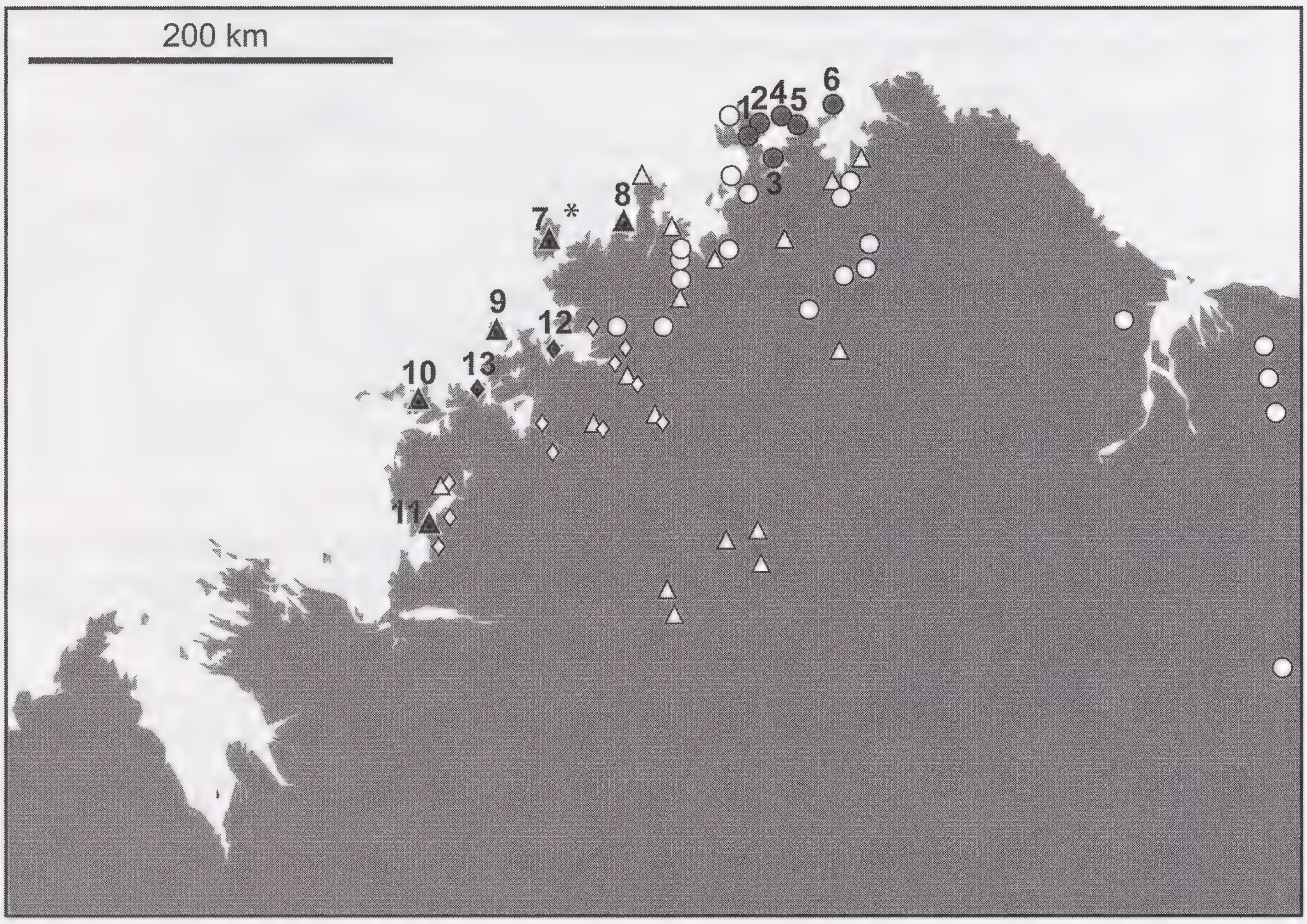

FIG. 57. Distribution map of *Xanthomelon* and *Globorhagada*. *Xanthomelon obliquirugosa*. Full circles = records treated herein: 1: Bougainville Peninsula, 2: Wargul Wargul Island, 3: Low and Jar Islands, 4: Long Island, 5: Mary Island, 6: Sir Graham Moore Island; white circles = records listed by Solem (1991). *Globorhagada prudhoensis* species complex: * = type locality of *G. prudhoensis* (Prudhoe Island); full triangles = records treated herein: 7: *Globorhagada prudhoensis* (Bigge Island), 8: ***Globorhagada confusa*** n. sp. (Katers Island), 9: *Globorhagada* sp. (Coronation Island), 10: ***Globorhagada wurroolgu*** n. sp. (Augustus Island), 11: ***Globorhagada yoowadan*** n. sp. (Storr Island); white triangles = records of *G. prudhoensis* listed by Solem (1991). *Globorhagada ruberpumilio* species complex: full diamonds = records treated herein: 12: ***Globorhagada wunandarra*** n. sp. (Boongaree Island), 13: ***Globorhagada uwinsensis*** n. sp. (Uwins Island); white diamonds = records of *G. ruberpumilio* listed by Solem (1991).

inner penial wall is a distinguishing character. In *Xanthomelon* penial wall pustules are present, from well developed to extremely fine, while in *Globorhagada* the wall lacks pustules, being smooth or supporting oblique lateral lamellae.

Distribution (Fig. 57)

Xanthomelon occurs in an area that reaches from the northern Kimberley (Prince Regent Reserve, Drysdale, Kalumburu) probably through to tropical Queensland. Stanisic et al. (2010) remarked that *Xanthomelon* might be polyphyletic. Accordingly, the range in Queensland remains uncertain in absence of a modern revision.

Xanthomelon obliquirugosa
(E. A. Smith, 1894)
Figs. 58A, 49–61

Helix (*Hadra*) *obliquirugosa* E. A. Smith, 1894: 90, pl. VII, fig. 17 (“Parry Harbour, northwestern Australia”).

Globorhagada obliquirugosa – Iredale, 1938: 114; 1939: 73, pl. 5, fig. 21.

Xanthomelon obliquirugosa – Solem, 1979: 35–42, pl. 1a, figs. 2a, b, 10a, b, 11a–d; 1985a: 921–922.

Type Locality

Northwestern Kimberley, Bougainville Peninsula, Parry Harbour, Vansittart Bay.

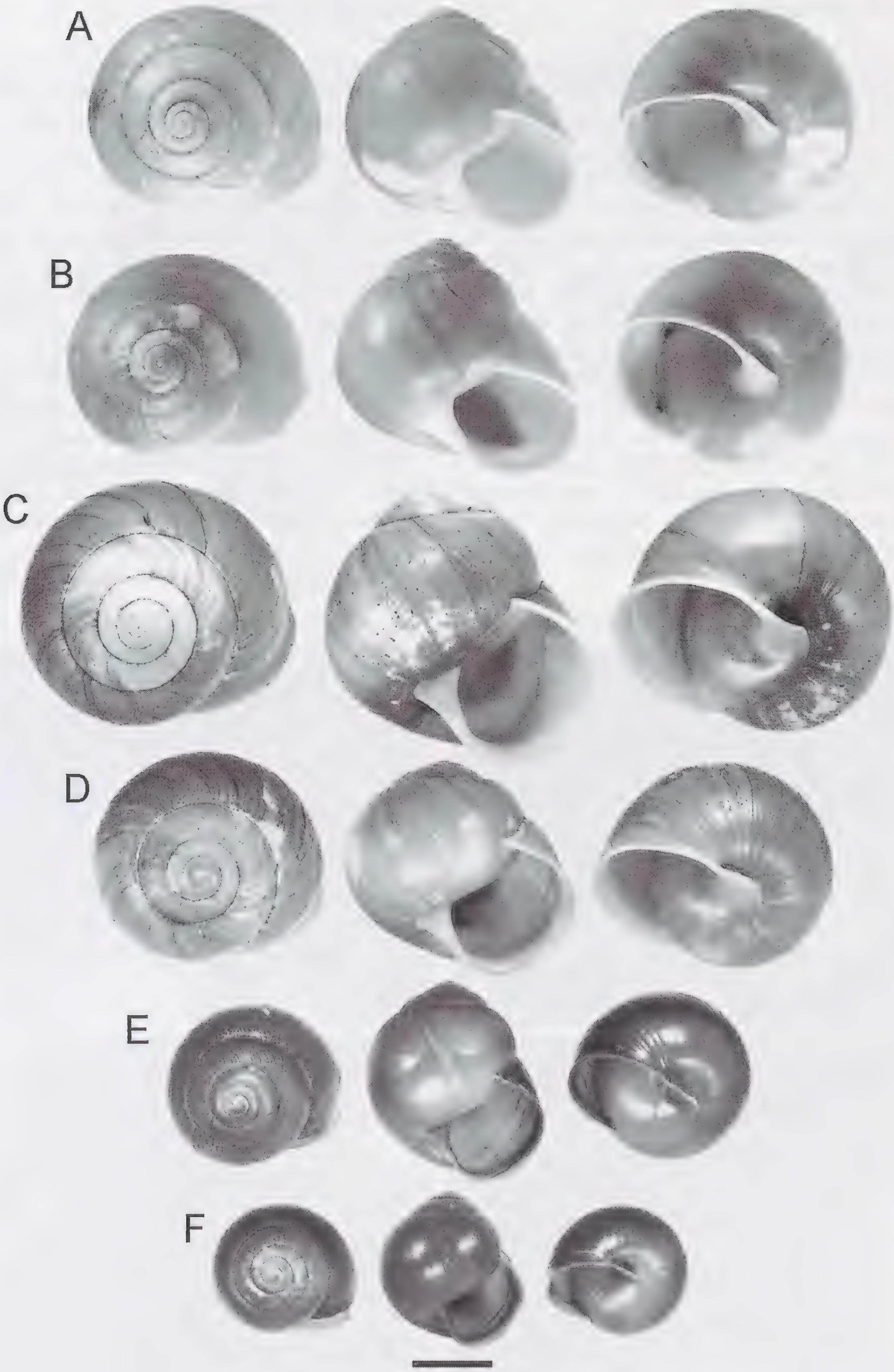

FIG. 58. Shells of *Xanthomelon* and *Globorhagada*. A: *Xanthomelon obliquirugosa* WAM S36532 (Sir Graham Moore Island); B: *Globorhagada prudhoensis* WAM S36507 (Bigge Island); C: ***Globorhagada confusa*** n. sp. holotype WAM S58483 (Katers Island); D: ***Globorhagada wurroolgu*** n. sp. holotype WAM S37631 (Augustus Island); E: ***Globorhagada wunandarra*** n. sp. paratype WAM S37624 (Boongaree Island); F: ***Globorhagada uwinsensis*** n. sp. paratype WAM S36994 (Uwins Island). Scale bar = 10 mm.

Taxonomic Remarks

The name *H. obliquirugosa* was introduced for dry shell material from Parry Harbour, Bougainville Peninsula, NW Kimberley (~ 14°00'S, 126°00'E). The lectotype BMNH 1892.1.29.159 was designated by Solem (1979). Subsequently, he described the anatomy based on specimens from various localities like Mitchell Plateau, Kalumburu and Drysdale River Reserve; none of these being very close to the type locality. Although Solem (1979) noticed considerable geographic variation with regard to shell size, he concluded that *X. obliquirugosa* is widespread ranging from the Prince Regent Reserve in the southwest to the Ningbing Ranges in the northeast. This assumption requires confirmation by future comparative studies, including molecular analyses. Here, for the first time anatomy of topotypic material is examined.

Material Examined

Non-type material AM C471735, WAM S36644–6, WAM 36849, WAM S58440 (9 preserved specimens), AM C471733–4, WAM S36514–32 (shells) from eastern and western sections of Sir Graham Moore Island, Eclipse Archipelago (13°53'S to 13°54'S, 126°35'E to 126°36'E); WAM S49349 (3 preserved specimens), WAM S49359 (5 preserved specimens), AM C471736, WAM S39330 (shells) from Mary Island in Vansittart Bay, 13°59'01–29"S, 126°22'45–59"E; WAM S49331–4 (shells) from Wargul Wargul Island, Vansittart Bay, 13°56'13.0"S, 126°10'27.5"E; WAM S49335 (shell) from Bougainville Peninsula, 13°55'58"S, 126°08'53"E; WAM S49336 (2 shells) from Low Island, Vansittart Bay, 14°09'52"S, 126°17'24"E; WAM S58440 (preserved specimen), WAM S49337 (6 shells) from Long Island, Eclipse Archipelago, Vansittart Bay, 13°56'04"S,

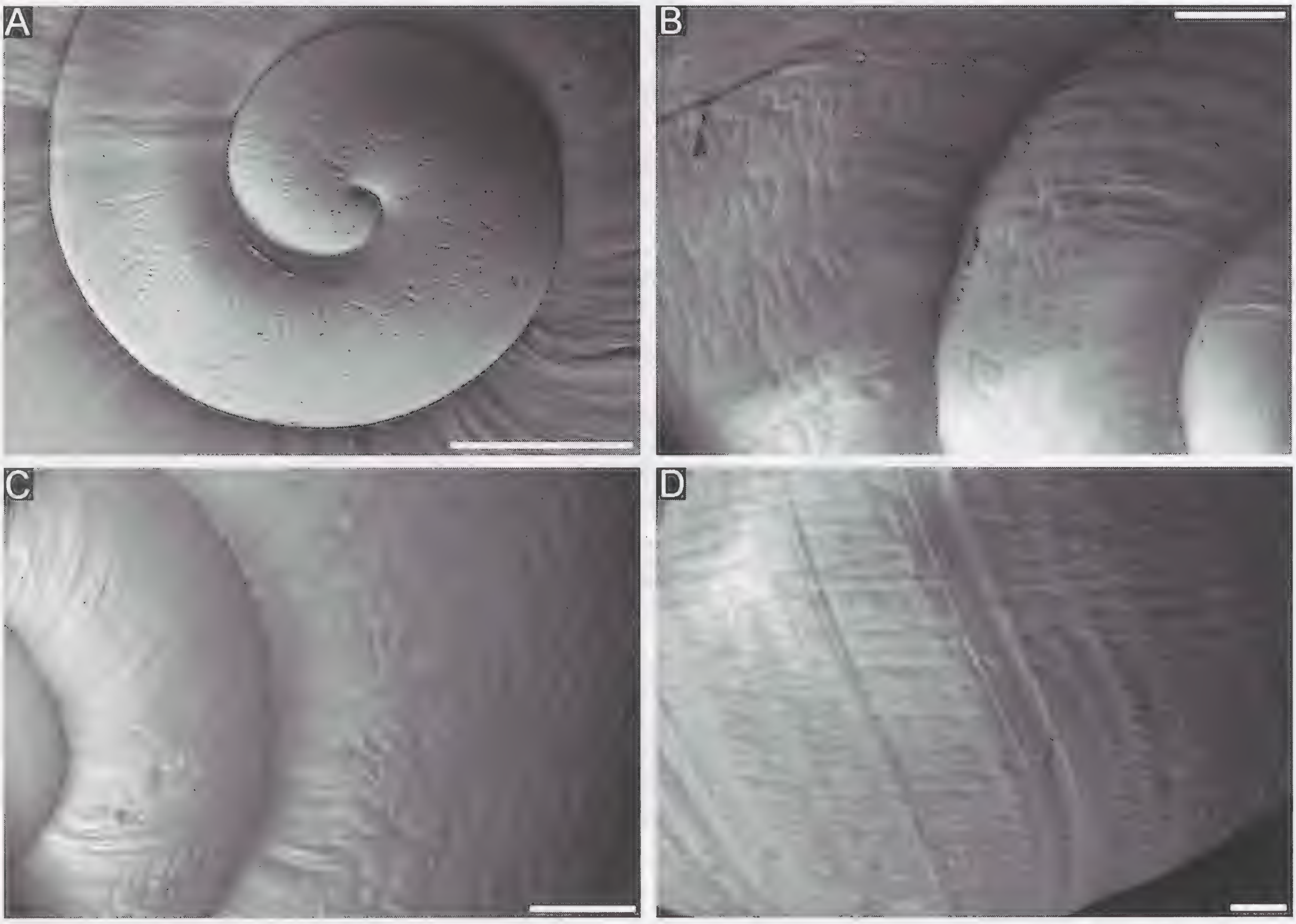

FIG. 59. SEM micrographs of *Xanthomelon obliquirugosa*. A: Apical view showing protoconch (AM C471736, Mary Island); B: Sculpture on first and second whorl (AM C471733, Sir Graham Moore Island); C: Sculpture on first and second whorl (WAM S36521, Sir Graham Moore Island); D: Sculpture on last whorl with typical oblique-radial pustulation (AM C471736, Mary Island). Scale bars = 1 mm.

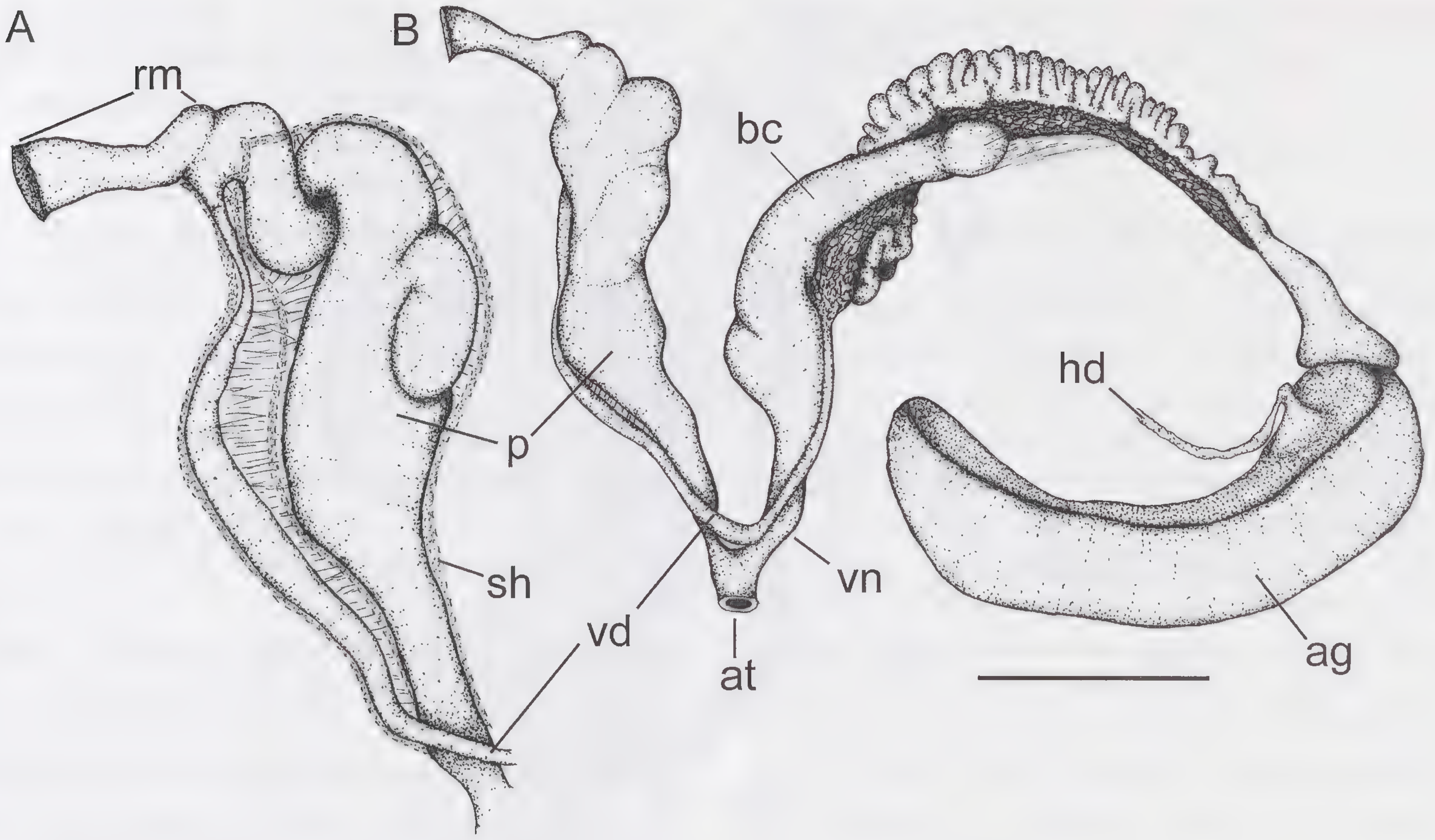

FIG. 60. Genital anatomy of *Xanthomelon obliquirugosa* WAM S36645 (Sir Graham Moore Island, August). A: Enlarged representation of penial complex showing coiling of penis within penial sheath; B: Entire genital system. Scale bar = 5 mm.

126°18'26"E; WAM S49228 (8 shells) from Jar Island, Vansittart Bay, 14°08'59"S, 126°14'10"E.

Diagnosis

Shell: Medium size to large (D = 20–30 mm, H = 18–30 mm), with moderately elevated spire, 3.7–5.0 rapidly increasing whorls; protoconch rather smooth with irregular growth lines; teleoconch with microscopic anastomosing radial rugosities that develop on second whorl continuing onto body whorl towards shell base, plus fine radial growth lines. Lip narrowly to strongly flared, white, sharply reflected, umbilicus forming a chink; colour light yellow-green, parietal callus thin, white (Figs. 58A, 59A–D).

Genital anatomy: Penis long, coiled, with thick glandular walls, inner wall entirely covered with extremely fine, dense pustulation, irregular longitudinal pilasters comprising entire length of wall, stimulatory pilaster lacking (Fig. 60). Vagina moderately long, tubular; bursa copulatrix thick, extending anterior end of spermoviduct with globular head; free oviduct shorter than vagina (Fig. 61) (modified from Solem, 1979).

Mitochondrial Differentiation

Infraspecific genetic divergence: 0.01 (4 sequences); mean p-distance to *X. durvillii* (3 sequences): 0.20.

Comparative Remarks

Compared with Solem's (1979) anatomical description based on material from various localities in the northern Kimberley, topotypic material examined here revealed no strikingly different features. However, more comprehensive studies of patterns of genetic and anatomical differentiation of populations across the entire range are needed for a proper delimitation of species. *Xanthomelon durvillii* differs by much weaker microsculpture of oblique radial corrugations and well-developed pustulation of inner penial wall, which also supports a main stimulatory pilaster. For comparison with species of *Globorhagada* refer to remarks given under the genus.

Distribution

Bougainville Peninsula and islands in Vansittart Bay, northern Kimberley. Reported from northernmost parts of Kimberley mainland between Prince Regent Reserve in the southwest and Ningbing Ranges in the northeast by Solem (1979).

Globorhagada Iredale, 1933

Globorhagada Iredale, 1933: 52; 1938: 114; 1939: 72–73. Type species: *Helix* (*Hadra*)

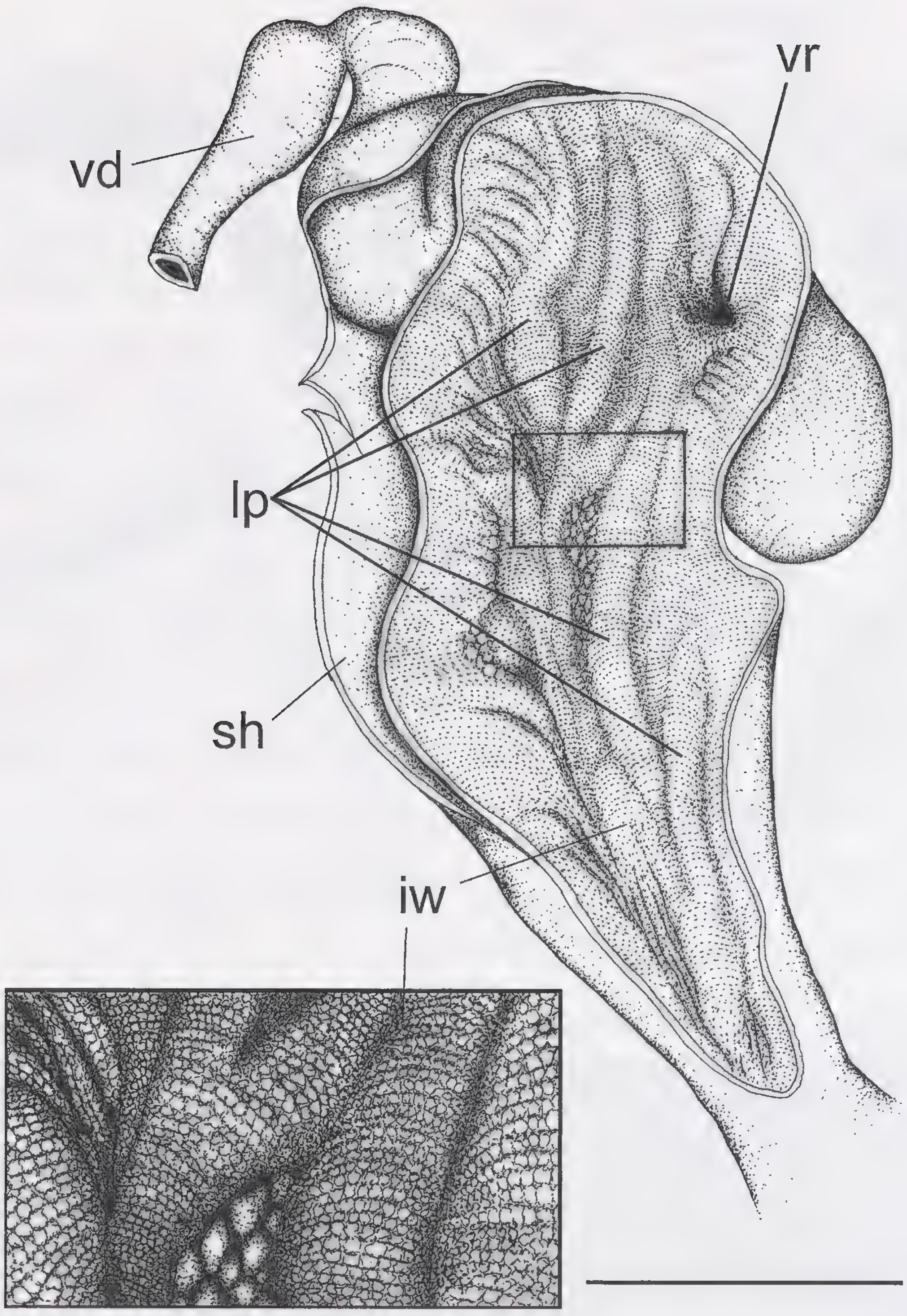

FIG. 61. Penial anatomy of *Xanthomelon obliquirugosa* WAM S36645 (Sir Graham Moore Island, August). Inset: 3-fold magnification of marked area of inner penial wall showing extremely fine pustulation. Scale bar = 3 mm.

prudhoensis E. A. Smith, 1894, by original designation.

Xanthomelon – Solem, 1979: 9–45 (partim); 1985a: 920–922 (partim); 1991: 175–178 (partim); Solem & McKenzie, 1991: 247–263 (partim).

Type Species

Helix (*Hadra*) *prudhoensis* E. A. Smith, 1894, by original designation.

Taxonomic Remarks

The name *Globorhagada* was validly introduced as subgenus within *Rhagada* by Iredale (1933), who provided a type species and a brief diagnosis ("large and globose, with open circular mouth, the columellar thickened, much reflected and appressed but not closing the umbilicus, a thick glaze joining the inner and outer lips"). None of these features are considered to be diagnostic for this genus, however. The taxon has subsequently been treated as a junior synonym of *Xanthomelon* (Solem, 1979). Herein, *Globorhagada* is removed from synonymy of *Xanthomelon* and elevated to the rank of a distinct genus while Iredale's (1933) description is being completed. Two previously recognised species, *G. prudhoensis* and *G. ruberpumilio* (Solem, 1979), are placed within that genus. Both taxa as delineated so far are considered to represent species complexes according to patterns of anatomical and mitochondrial differentiation unrevealed by comparative studies of material from several localities in the Kimberley.

Diagnosis

Shell: Large to very large (D = 16–36 mm; Table 4), moderately thick, globose, strongly elevated, H/D ratio averaging 1.0; umbilicus partly concealed; protoconch from rather smooth to sculptured with faint radial growth lines; teleoconch sculpture variable, with axial rows of more or less well-developed pustulation, prominence decreased near sutures; body whorl strongly enlarged, descending slightly but abruptly behind apertural lip; whorls rapidly increasing, separated by shallow suture; periphery well rounded to slightly depressed; aperture wide, columellar margin and parietal wall weakly to strongly callued. Shell colour more or less uniform, yellowish to dark brown, no colour banding.

Radula: 3.5–5.5 mm long; C + 16–32 + 3–4 + 20–36.

Genital anatomy: Penis with well-developed sheath, extending entire length, thick proximally, thin distally; penis straight or coiled within sheath, inner penial wall lacking well-differentiated main pilaster, usually with oblique lamellae, exceptionally also smooth, but never with pustulation; epiphallus lacking; penial retractor muscle attached to junction with vas deferens. Vas deferens entering penial sheath distally, entering penial chamber through simple pore. Bursa copulatrix simple, with globular head, reaching or extending base of spermoviduct.

Aestivation Strategy

Free sealer.

Comparative Remarks

The shell of *Globorhagada* reveals no apparent feature to distinguish it from *Xanthomelon*. A different microsculpture of the teleoconch (axial rows of tiny pustules instead of oblique corrugations) and distinct armature of the inner penial wall (oblique lamellae instead of pustules), and vas entering penial sheath distally instead of proximally are considered to be the main differentiating features. From all other camaenid taxa, *Globorhagada* is readily distinguished by large, globose, mostly yellowish shell with flaring aperture. Two species have been recognised, *G. prudhoensis* and *G. ruberpumilio*, which are easy to differentiate by distinct shell and penial anatomy. Patterns of anatomical and mitochondrial differentiation suggest that both taxa represent complexes of anatomically similar species, which are characterised by rather subtle differences in shell and penial anatomy. Interspecific genetic p-distances within each complex (0.04–0.09) are about an order of magnitude larger than infraspecific genetic p-distances (0.002–0.012) and an order of magnitude smaller than mean genetic distance between species complexes (0.23).

Diversity and Distribution (Fig. 57)

Species of *Globorhagada* occur in most of the Kimberley between the Drysdale River Reserve in the northeast and the Doubtful Bay area in the southwest; mostly at localities within 60 km distance from the coast; distribution in the interior and east Kimberley unclear. Distribution overlaps with *Xanthomelon* in northern Kimberley (Prince Regent, Kalumburu, Drysdale River areas). Herein, four species are recognised within *G. prudhoensis* species complex that occur on Bigge, Katers, Augustus and Storr islands, respectively, including adjacent areas and/or islands. Shell fragments that do not permit species identification were also found on northern section of Coronation Island, 14°58'14–30"S, 124°54'24–31"E (WAM S37385–6). Within the *G. ruberpumilio* compex, two species are newly described from Boongaree and Uwins islands, respectively, in addition to *G. ruberpumilio*. Hence, current number of *Globorhagada* species is seven.

Globorhagada prudhoensis Complex

This complex contains species with similar shells that are characterised by distinct penial wall anatomy and separated by relatively low infraspecific p-distances 16S.

Globorhagada prudhoensis
(E. A. Smith, 1894)
Figs. 58B, 62–64

Helix (*Hadra*) *prudhoensis* E. A. Smith, 1894: 91, pl. VII, fig. 9 ("Prudhoe Island, northwestern Australia").

Globorhagada prudhoensis – Iredale, 1938: 114, Iredale, 1939: 72, pl. 5, fig. 19 (not *Xanthomelon prudhoensis* – Solem, 1979: 35–42, pl. 1a, figs. 2a, b, 10a, b, 11a–d, Solem, 1985a: 921–922).

Type Locality

Northwestern Kimberley, Bonaparte Archipelago, Montague Sound, Prudhoe Island (~ 14°25'10"S, 125°15'48"E).

Taxonomic Remarks

Description based on two leached and worn shells; Solem (1979) designated the lectotype

BMNH 1892.1.29.165. The anatomy was described by Solem (1979) based on specimens from mainland localities, such as Mitchell Plateau, Prince Regent Reserve, and Kalumburu, which exhibited similar features across a large range on the mainland. Furthermore, Solem (1979) assumed that mainland populations were conspecific with the types from Prudhoe Island. However, this study revealed that offshore islands harbour distinct species, which are recognised by different anatomy of the inner penial wall. A distinct species was also found on Bigge Island, which is in close proximity of Prudhoe Island (about 10 km to the west). It is considered more likely that the Bigge Island population is conspecific with the types than the mainland populations from a larger distance studied by Solem (1979). It is therefore concluded that Solem's (1979) description does not refer to the taxon described by Smith (1894) but to a distinct, yet unnamed species. The description of *G. prudhoensis* is corrected accordingly based on description of material from Bigge Island.

Material Examined

AM C471852, WAM S36636–43, WAM S36760, WAM S36850–5 (preserved specimens), AM C471853, WAM S36443, WAM S36450, WAM S36502–13, WAM S36954–6 (shells) from Bigge Island, 14°35'00"–20'5"S, 125°05'57"–11'24"E.

Description

Shell (Figs. 58B, 62A–C, Table 4): Very large, globose to broadly conical, with well-to strongly elevated spire, body whorl largely expanded with compressed periphery, well rounded below, slightly shouldered above, suture relatively shallow; colour evenly yellowish green, inner lip whitish. Protoconch ~ 4.2 mm in diameter, comprising 1–1.5 whorls, with faint radial lirae

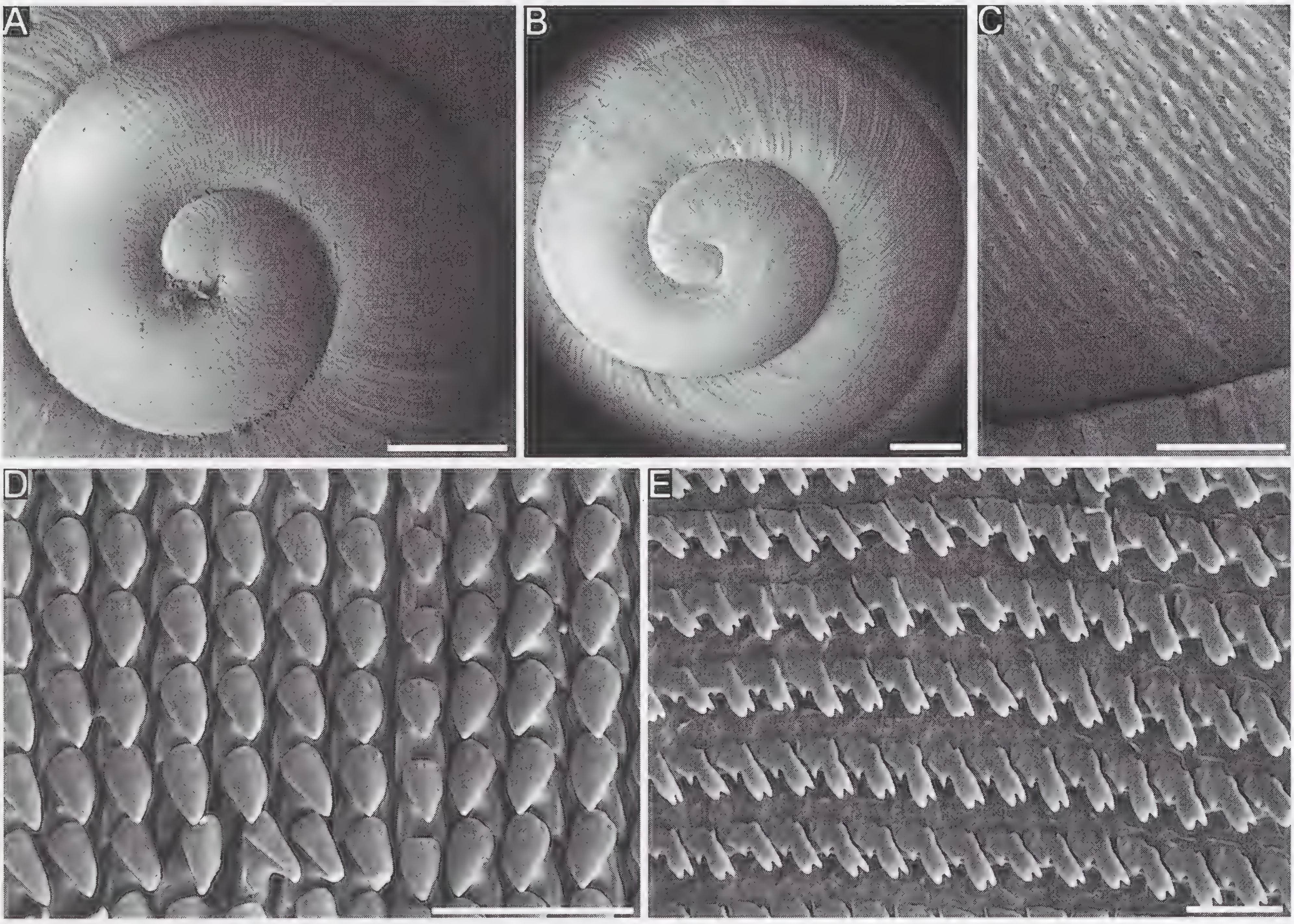

FIG. 62. SEM micrographs of *Globorhagada prudhoensis* (Bigge Island). A–C: Shell. Scale bars = 1 mm. A: Apical view showing protoconch (WAM S36443); B: Apical view showing sculpture on first whorl (AM C471853); C: Detail of sculpture on penultimate whorl with typical axial corrugation (WAM S36510); D–E: Radula (AM C471855); D: Central and inner lateral teeth viewed from above. Scale bar = 100 µm; F: Close-up of middle and outer marginal teeth. Scale bar = 50 µm.

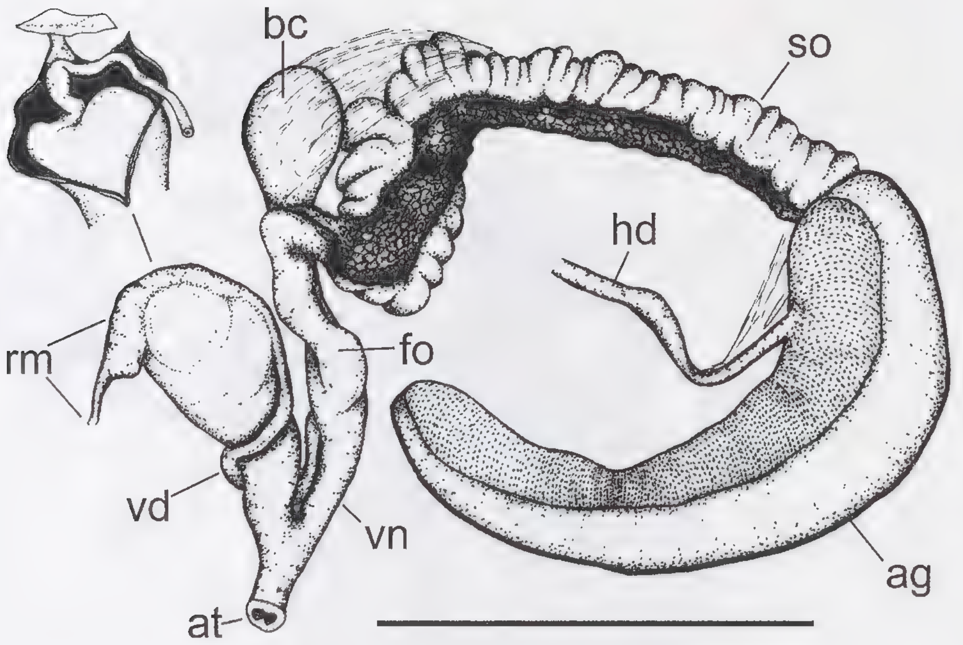

FIG. 63. Genital anatomy of *Globorhagada prudhoensis* WAM S36641 (Bigge Island, July), inset showing detail of penial apex with penial sheath removed. Scale bar = 10 mm.

only. Teleoconch with regular, faint axial growth lines supporting rows of tiny pustulation, evenly distributed across shell, reduced at base. Umbilicus narrowly open, up to 4 mm wide, partly concealed (0 to 90%). Aperture well rounded, wide, simple, moderately thick, basal node weak to absent, palatal node absent, parietal wall thin, white.

Radula (Fig. 62D–E): 3.5–5.5 mm long; C + 24–32 + 3–4 + 26–36.

Genital anatomy (Figs. 63–64): Penis long, cylindrical, not coiled within penial sheath, with thick glandular walls. Vas entering penis through relatively wide, collar-shaped vergic ring located in apical portion of penial chamber; inner wall with complex patterns of laterally corrugated, crescent-shaped pads that form around a central gutter running longitudinally along inner surface of penial wall, no main stimulatory pilaster. Vagina moderately long, tubular. Bursa copulatrix thick with well-globular head, slightly extending anterior end of spermoviduct.

Mitochondrial Differentiation

Mean infraspecific sequence divergence 0.002 (3 sequences); mean p-distances to other species of the *G. prudhoensis*-complex between 0.07 and 0.09; mean p-distances to species of the *G. ruberpumilio*-complex 0.23–0.27.

Comparative Remarks

Anatomical description based on dissection of two specimens. The most significant difference compared to Solem's (1979) description of the mainland species is the very distinct inner penial wall sculpture, which is considered to justify recognition of both taxa as distinct species. Species of the *G. prudhoensis* complex do not vary significantly in their shell with amount of variation within local populations being comparable to that between species.

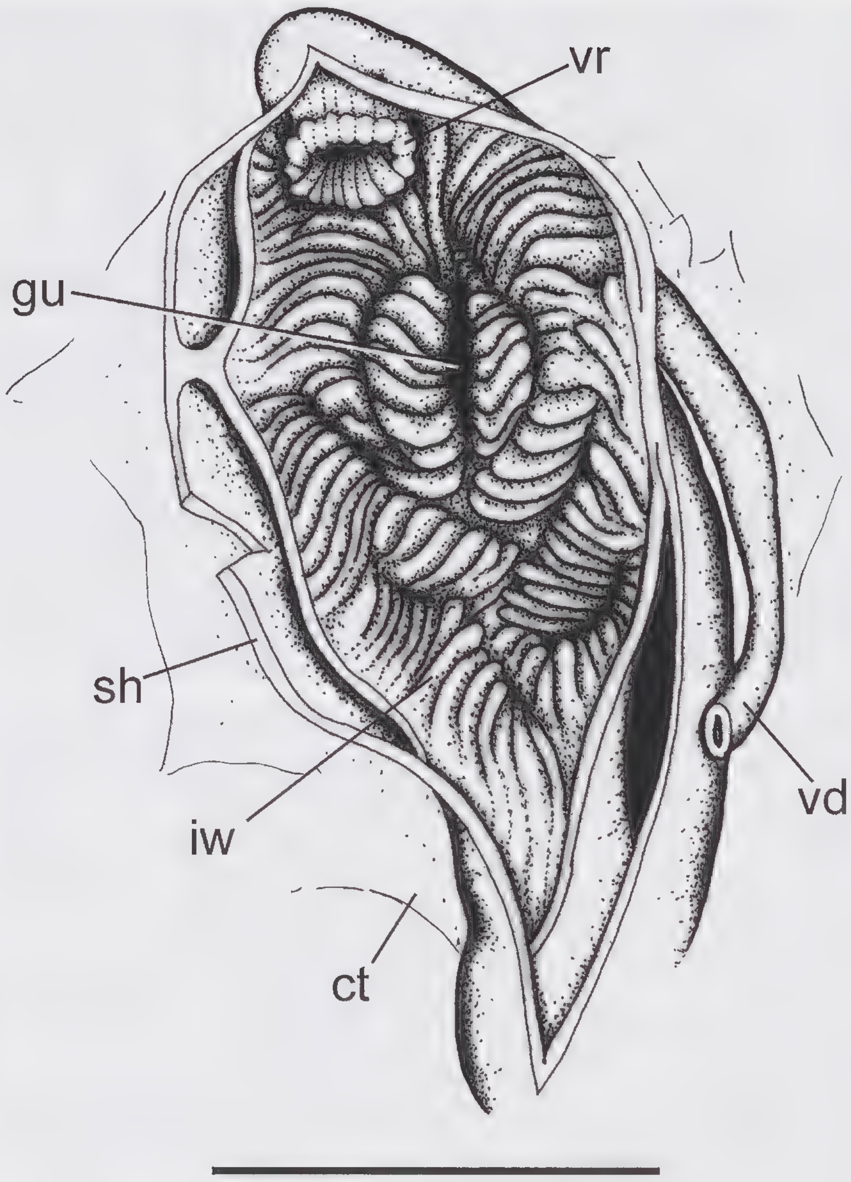

FIG. 64. Penial anatomy of *Globorhagada prudhoensis* WAM S36641 (Bigge Island, July). Scale bar = 3 mm.

Distribution (Fig. 57)

Prudhoe and Bigge islands; in contrast to earlier accounts (Solem, 1979, 1991), not known from the Kimberley mainland.

Globorhagada confusa n. sp.
Figs. 58C, 65–67

Xanthomelon prudhoensis – Solem, 1979: 35–42, pl. 1a, figs. 2a, b, 10a, b, 11a–d; 1985a: 921–922) (not *Helix* (*Hadra*) *prudhoensis* E. A. Smith, 1894).

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Montage Sound, W coast of Katers Island, 14°26'56.5"S,

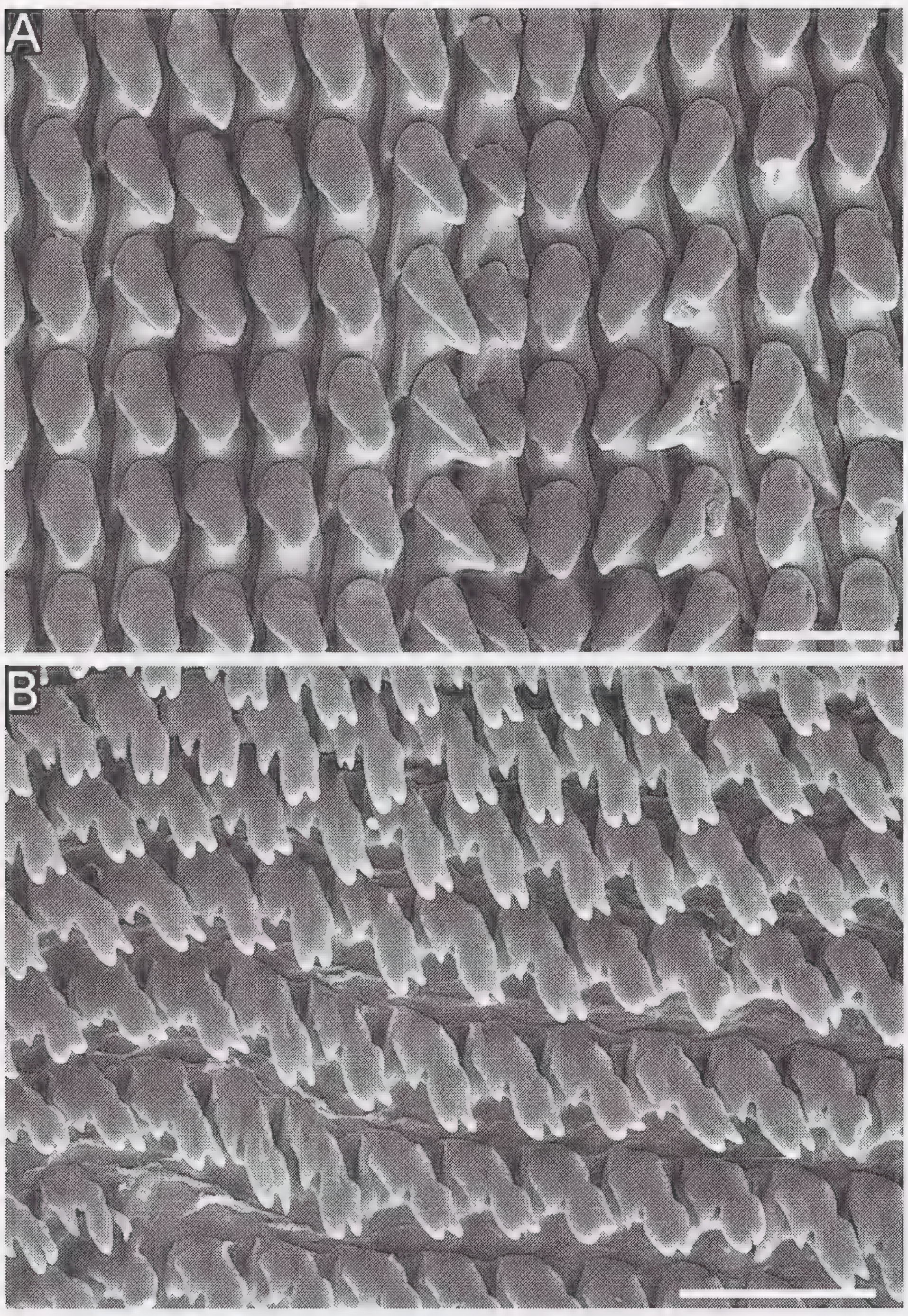

FIG. 65. SEM micrographs of the radula of ***Globorhagada confusa*** n. sp. paratype WAM S36856 (Katers Island). A: Central and inner lateral teeth viewed from above; B: Marginal teeth viewed from above. Scale bars = 50 µm.

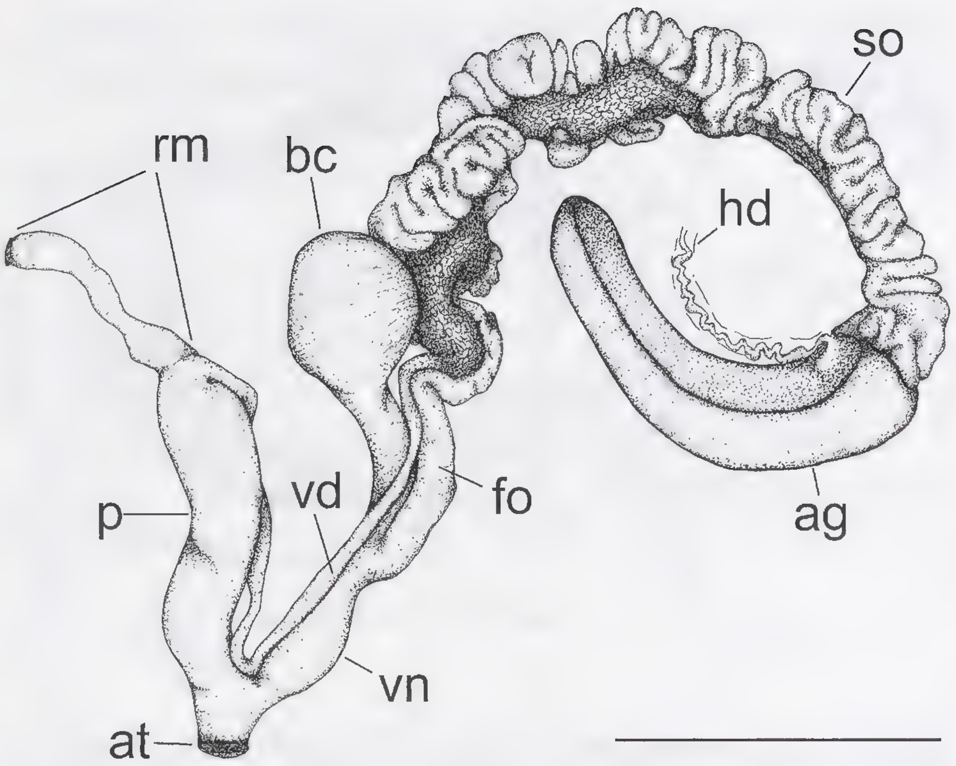

FIG. 66. Genital anatomy of ***Globorhagada confusa*** n. sp. paratype WAM S36856 (Katers Island, February). Scale bar = 10 mm.

125°31’22.7”E; coll. Paul Doughty, 14/02/2008, KIS 2–36 (in caves and near ledges on sandstone; active on ground at night after rain).

Taxonomic Remarks

When Solem (1979, 1991) described the anatomy of the present species as based on specimens from around Kalumburu Mission, he assumed it was identical with the taxon from Prudhoe Island named “*H. prudhoensis*” by Smith (1894). Here, evidence is presented that Solem’s (1979) description refers to a distinct species and that the name “*prudhoensis*” was incorrectly applied. Because no other name is available, the new species ***G. confusa*** is herein described for material from Katers Island. The anatomy of specimens from Katers Island fit well Solem’s anatomical description of material from Kalumburu. Material from both localities is thus considered conspecific. Solem’s (1979) description of “*Xanthomelon prudhoensis*” as well as the notion of a wide mainland distribution of this species in the Kimberley refers to the present species.

Material Examined

Holotype WAM S58483 (preserved specimen, Fig. 58C). Paratypes AM C471857 (preserved specimen, dissected), WAM S36856 (preserved specimen), WAM S36451 (juvenile shell), WAM S36966 (worn shell), WAM S36973 (worn shell) from west coast of Katers Island, 14°26’45.6” to 14°26’59.4”S, 125°30’53.9” to 125°31’22.7”E.

Etymology

The name refers to the confusion of this species with *G. prudhoensis* by Solem (1979).

Description

Shell (Fig. 58C; Table 4): Very large, globose to broadly conical, with well to strongly elevated spire, body whorl largely expanded with compressed periphery, well rounded below, slightly shouldered above, suture shallow; colour evenly yellowish green, inner lip whitish. Protoconch about 4.2 mm in diameter, comprising 1–1.5 whorls, with faint radial lirae only. Teleoconch with regular, faint axial growth lines supporting axial rows of tiny pustulation, evenly distributed across shell, reduced at base. Umbilicus up to 4 mm wide, partly concealed (0 to 90%). Aperture well rounded, wide, simple,

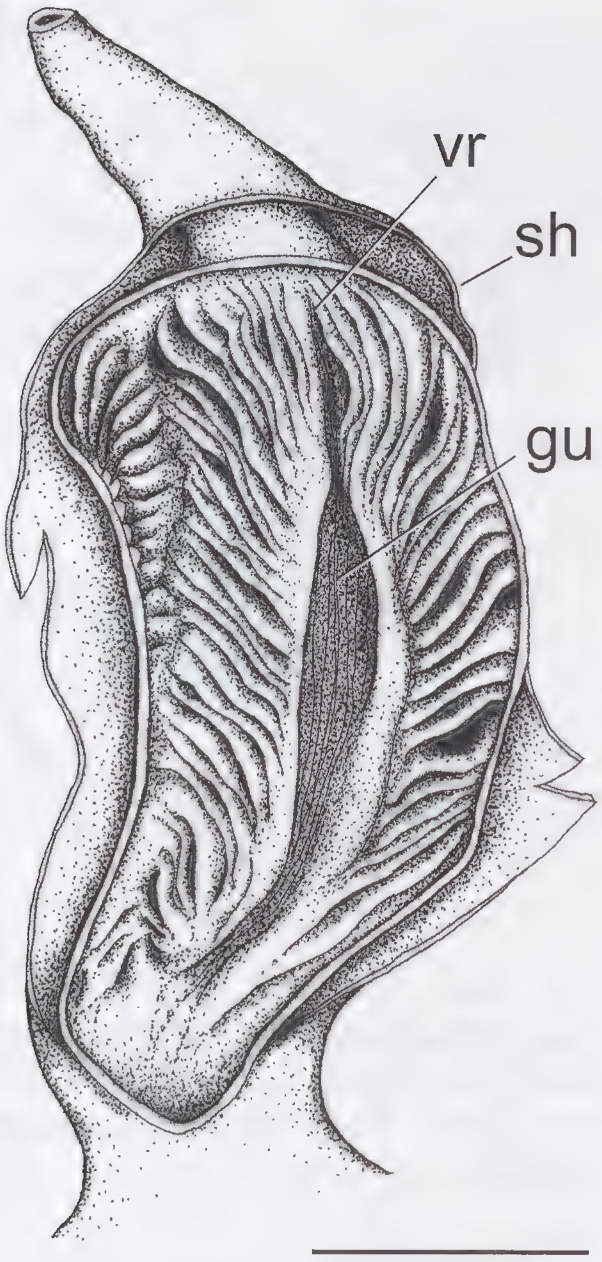

FIG. 67. Penial anatomy of **Globorhagada confusa** n. sp. paratype WAM S36856 (Katers Island, February). Scale bar = 3 mm.

moderately thick, basal node weak to absent, palatal node absent, parietal wall thin, white.

Radula (Fig. 65): 4.7 mm long with 135 rows of teeth, C + 24+ 3–4 + ~ 30 (n = 1).

Genital anatomy (Figs. 66–67): Penis tubular, not coiled within penial sheath, with thick, glandular walls. Vas entering penial sheath within distal third of penial complex, entering penial chamber through wide, simple pore that gives rise to a sperm gutter running along entire inner penial wall; narrow, obliquely lateral lamellae form on both sides of gutter. Vagina moderately long, tubular. Bursa copulatrix thick, head globular, slightly extending anterior end of spermoviduct.

Mitochondrial Differentiation

Mean infraspecific sequence divergence 0.002 (3 sequences); mean p-distances to other species of the *G. prudhoensis*-complex between 0.04 and 0.09; mean p-distances to species of the *G. ruberpumilio*-complex 0.21–0.24.

Comparative Remarks

Anatomical description based on dissection of two specimens. Anatomy described here corresponds well with Solem's (1979) description of "*Xanthomelon prudhoensis*" from NW Kimberley mainland, confirming that Katers Island population is conspecific with mainland form (Katers Island being separated from mainland by a narrow strait only). It differs most conspicuously from *G. prudhoensis* by inner penial wall sculpture consisting of obliquely radial lamellae instead of transversely corrugated, crescent-shaped pilasters. In addition, vas deferens enters penial lumen through wide, simple pore instead of collar-like vergic ring. Only three adults available from Katers Island. These differ from *G. prudhoensis* by larger size (H = 35.1 mm on average instead of 30.4 mm; Table 4). However, number of measured specimens is too small to allow for statistically significant comparison. Solem (1979) provided measurements of a large number of specimens ranging in height between 24.6 and 35.1 mm.

Distribution (Fig. 57)

According to Solem (1979), fairly widespread on mainland from Drysdale River Reserve in the northeast to Prince Regent Reserve in the southwest, including Kalumburu and Mitchell Plateau, plus Katers Island.

Globorhagada wurroolgu n. sp.

Figs. 58D, 68, 69

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, northwestern section of Augustus Island, 15°20'11"S, 124°31'10"E; coll. Vince Kessner, 13/02/2009, KIS 1–67 (open woodland on moderately steep W-facing slopes at base of sandstone cliffs; active after rain).

Material Examined

Holotype WAM S37631 (preserved specimen, dissected, Fig. 58D). Paratypes AM C471858 (preserved animal) from type locality; WAM S37380 (shell), WAM S37381 (shell), WAM S37382 (shell), WAM S37387 (2 shells), WAM S37388 (shell), WAM S49013 (2 shells) from northwestern section of Augustus Island; WAM S37632 (preserved specimen) from eastern

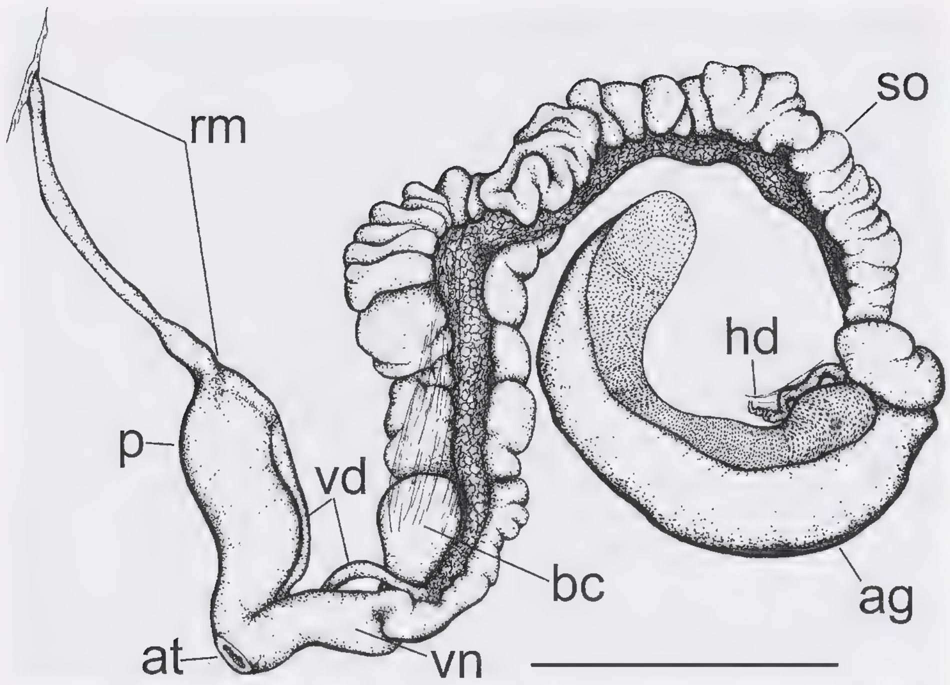

FIG. 68. Genital anatomy of ***Globorhagada wurroolgu*** n. sp. holotype WAM S37631 (Augustus Island, February). Scale bar = 10 mm.

section of Champagny Island, 15°17’42”S, 124°16’39”E.

Additional, non-type material WAM S37383 (shell), WAM S37384 (2 shells), WAM S37389 (shell) from central section of D’Arcy Island, 15°17’22–31”S, 124°24’4–11”E.

Etymology

For Wurroolgu, name of Augustus Island in Worrorra, language of the Dambimangari people; noun in apposition.

Description

Shell (Fig. 58D, Table 4): Very large, globose to broadly conical, with well- to strongly elevated spire, body whorl largely expanded with compressed periphery, well rounded below, slightly shouldered above, suture relatively shallow; colour evenly yellowish green, inner lip whitish. Protoconch about 4.2 mm in diameter, comprising 1–1.5 whorls, with faint radial lirae only. Teleoconch with regular, faint axial growth lines supporting axial rows of tiny pustulation, evenly distributed across shell, reduced at base. Umbilicus forming chink. Aperture well rounded, wide, simple, moderately thick, basal node weak to absent, palatal node absent, parietal wall thin, white.

Genital anatomy (Figs. 68, 69): Penis tubular, not coiled within penial sheath, with thick glandular walls. Vas entering penial sheath within distal third of penial complex, entering penis through wide, simple pore that gives rise to a sperm gutter on distal half of inner penial wall; inner penial wall completely covered with narrow, regular, crowded, longitudinal lamellae that run almost parallel to this gutter. Anteriorly to these lamellae, strong, irregular pilasters or cords are forming on both sides of gutter running oblique- longitudinally in a sharp V-shaped direction. Vagina moderately long, tubular. Bursa copulatrix thick, with globular head, slightly extending anterior end of spermoviduct.

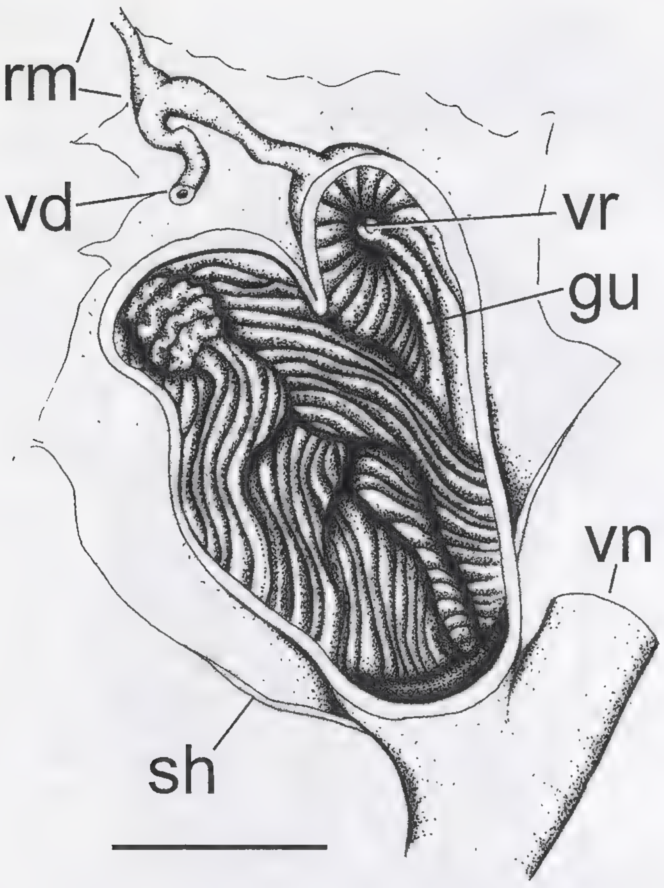

FIG. 69. Penial anatomy of ***Globorhagada wuroolgu*** n. sp. holotype WAM S37361 (Augustus Island, February). Scale bar = 3 mm.

Mitochondrial Differentiation

Mean infraspecific sequence divergence 0.003 (one sequence each from Augustus and Champagny Islands); mean p-distances to other species of the *G. prudhoensis*-complex between 0.04 and 0.09; mean p-distances to species of the *G. ruberpumilio*-complex 0.23–0.24.

Comparative Remarks

Anatomical description based on dissection of two specimens. Differs most conspicuously from *G. prudhoensis* and ***G. confusa*** by distinct armature of inner penial wall, which exhibits lateral lamellae and oblique pilasters, while *G. prudhoensis* has crescent shaped, corrugated pads and ***G. confusa*** oblique lamellae. Shells of *G.* ***wurroolgu*** are smaller than those of former two species (Table 4).

Distribution (Fig. 57)

Northwestern section of Augustus Island and Champagny Island. Shells from D'Arcy Island, located in between these islands, are considered conspecific. Not found so far in southern part of August Island.

Globorhagada yoowadan n. sp.
Figs. 70, 71

Type Locality

Western Australia, southwestern Kimberley, Doubtful Bay, southeastern section of Storr Island, 15°57'02"S, 124°33'39"E; coll. Vince Kessner, 20/05/2009, KIS 3–137 (dry vine thicket patch on S-facing sandstone ridge; under rocks).

Material Examined

Holotype WAM S58484 (preserved specimen). Paratypes AM C471859 (preserved animal, dissected), WAM S37735–7 (3 preserved specimens), WAM S37796–801 (8 shells) from southeastern section of Storr Island.

Additional, non-type material WAM S37738 (preserved specimen) WAM S37791 (preserved specimen), WAM S37862–4 (3 shells), WAM S37866 (3 shells) from unnamed island in Doubtful Bay, 15°54'36"–55'08"S, 124°27'39–53"E.

Etymology

For Yoowadan, name of Storr Island in Worrorra, language of the Dambimangari people; noun in apposition.

Description

Shell (Table 4): Very large, globose to broadly conical, with well- to strongly elevated spire, body whorl largely expanded with compressed periphery, well rounded below, slightly shouldered above, suture relatively shallow; colour evenly yellowish green, inner lip whitish. Protoconch about 4.2 mm in diameter, comprising 1–1.5 whorls, with faint radial lirae only. Teleoconch with regular, faint axial growth lines supporting axial rows of tiny pustulation, evenly distributed across shell, reduced at base. Umbilicus forming a chink. Aperture well rounded, wide, simple, moderately thick, basal node weak to absent, palatal node absent, parietal wall thin, white.

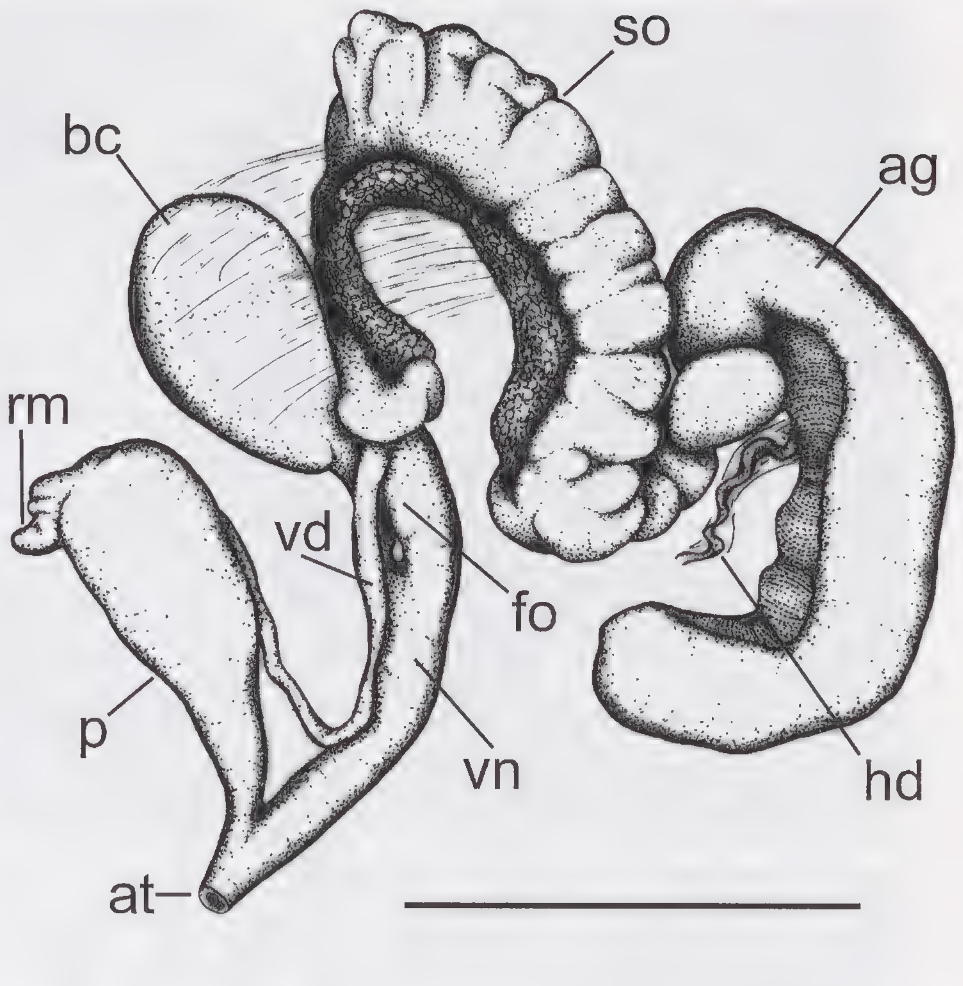

FIG. 70. Genital anatomy of ***Globorhagada yoowadan*** n. sp. holotype WAM S58484 (Storr Island, May). Scale bar = 10 mm.

Genital anatomy (Figs. 70–71): Penis long, cylindrical, not coiled within penial sheath, with thick glandular walls. Vas entering penial sheath within distal third of penial complex, entering penial lumen through wide, simple pore; inner penial wall completely covered with narrow, regular, crowded, obliquely longitudinal lamellae that run in a sharp V-shaped direction, forming a gutter; lamellar fields extending from distal end to near proximal end of interior wall, ending abruptly within proximal fifth of wall. Vagina long, tubular; bursa copulatrix thick, head hugely expanded, globular, slightly extending anterior end of spermoviduct, connected to spermoviduct by connective tissue; free oviduct shorter than vagina; spermoviduct and albumen gland typical.

Mitochondrial Differentiation

Mean infraspecific sequence divergence 0.011 (four sequences, three from Storr Island, one from unnamed island, Doubtful Bay); mean p-distances to other species of the *G. prudhoensis*-complex between 0.04 and 0.09; mean p-distances to species of the *G. ruberpumilio*-complex 0.21–0.24.

Comparative Remarks

No shell photos taken as holotype was cracked for dissection and other shells are not fully mature or worn. Anatomical description

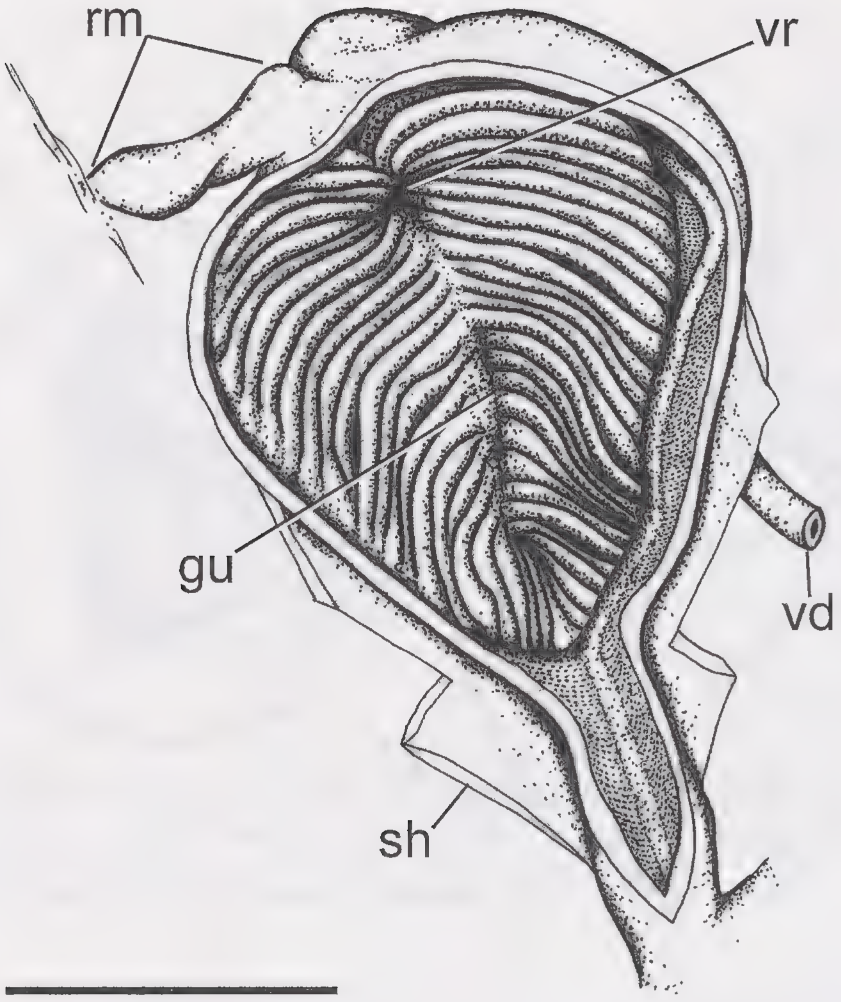

FIG. 71. Penial anatomy of ***Globorhagada yoowadan*** n. sp. holotype WAM S58484 (Storr Island, May). Scale bar = 10 mm.

based on dissection of one specimen. Differs most conspicuously from *G. prudhoensis* by distinct armature of inner penial wall, which exhibits oblique lamellae, while *G. prudhoensis* has crescent shaped, corrugated pads; similar to ***G. confusa*** with weaker sperm gutter, lamellae more regular and finer. Shells of ***G. yoowadan*** are slightly smaller than those of former two species (Table 4).

Distribution (Fig. 57)

Known from Storr Island and unnamed island in Doubtful Bay, probably also to be found on adjacent mainland.

Globorhagada ruberpumilio Complex

This complex contains species with similar shells that are characterised by distinct penial wall anatomy and separated by relatively low infraspecific genetic p-distances in 16S.

Globorhagada wunandarra n. sp.

Figs. 58E, 72–74

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04’15”S, 125°11’14”E; coll. Michael Shea, 9/08/2007, KIS 1–30 (sandstone boulders, dry woodland, vine thicket-grassland mix; sealed to bark under tree).

Material Examined

Holotype WAM S36635 (preserved specimen, dissected). Paratypes AM C471861 (6 preserved specimens), WAM S37623 (3 preserved specimens), WAM S37624 (15 preserved specimens), WAM S37625 (preserved specimen), WAM S36634 (preserved specimen), AM C471860 (shell), WAM S36446–8 (6 shells), WAM S36487 (shell), WAM S36952 (shell) from central section of Boongaree Island.

Etymology

For Wunandarra, name of Boongaree Island in Wunambal, language of the Uunguu people; noun in apposition.

Description

Shell (Figs. 58E, 72A–D, Table 4): Moderate in size (small for the genus), globose, with highly elevated spire, last whorl extremely increased in height and diameter, accounting for two thirds of entire shell height, depressed at periphery, well rounded below, slightly shouldered above; suture shallow. Protoconch 3.4 mm in diameter, comprising about one whorl, essentially smooth with only faint radial growth lines. Teleoconch with conspicuous sculpture on upper half of whorls consisting of delicate axial growth lines that support dense axial rows of microscopic pustules, particularly prominent on penultimate and last whorl, pustulation absent from lower part of last whorl and base of shell. Colour chestnut brown with beige to light brown suffusion at base of shell, outer lip colour may be darker than shell, inner lip purplish brown. Umbilicus partly to almost completely concealed, forming a narrow opening or chink. Apertural lip well rounded, simple, flaring, sharp, nodes absent, parietal wall inconspicuous.

Radula (Fig. 72E, F): 3.5–5.5 mm long; C + 18 + 3–4 + 10–22.

Genital anatomy (Figs. 73–74): Penis long, cylindrical, not coiled within penial sheath, with thick glandular walls. Vas entering penial sheath within distal third of penial complex, opening into penial lumen through a simple pore; interior penial wall densely covered with extremely minute pustules, one smooth,

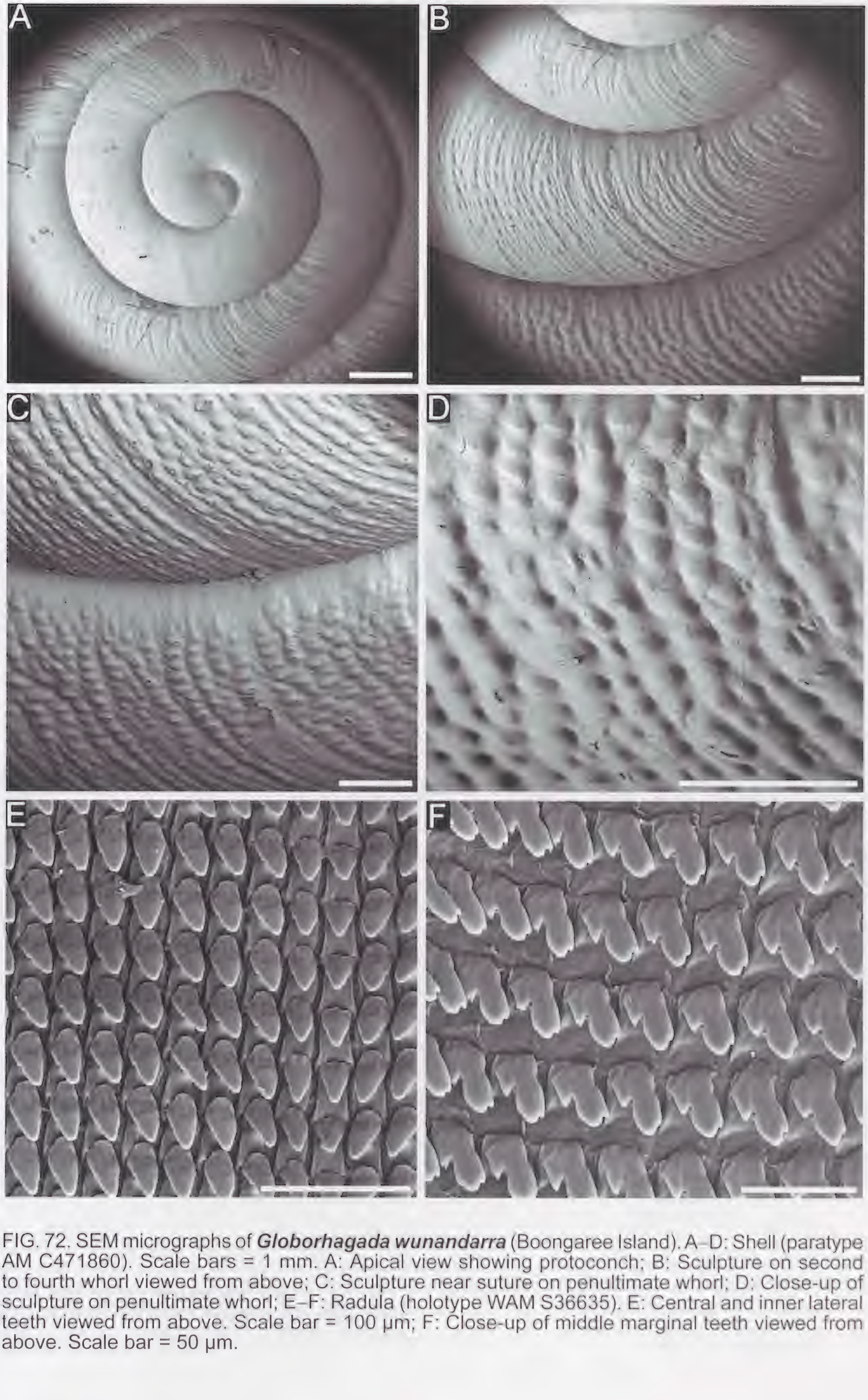

FIG. 72. SEM micrographs of ***Globorhagada wunandarra*** (Boongaree Island). A–D: Shell (paratype AM C471860). Scale bars = 1 mm. A: Apical view showing protoconch; B: Sculpture on second to fourth whorl viewed from above; C: Sculpture near suture on penultimate whorl; D: Close-up of sculpture on penultimate whorl; E–F: Radula (holotype WAM S36635). E: Central and inner lateral teeth viewed from above. Scale bar = 100 µm; F: Close-up of middle marginal teeth viewed from above. Scale bar = 50 µm.

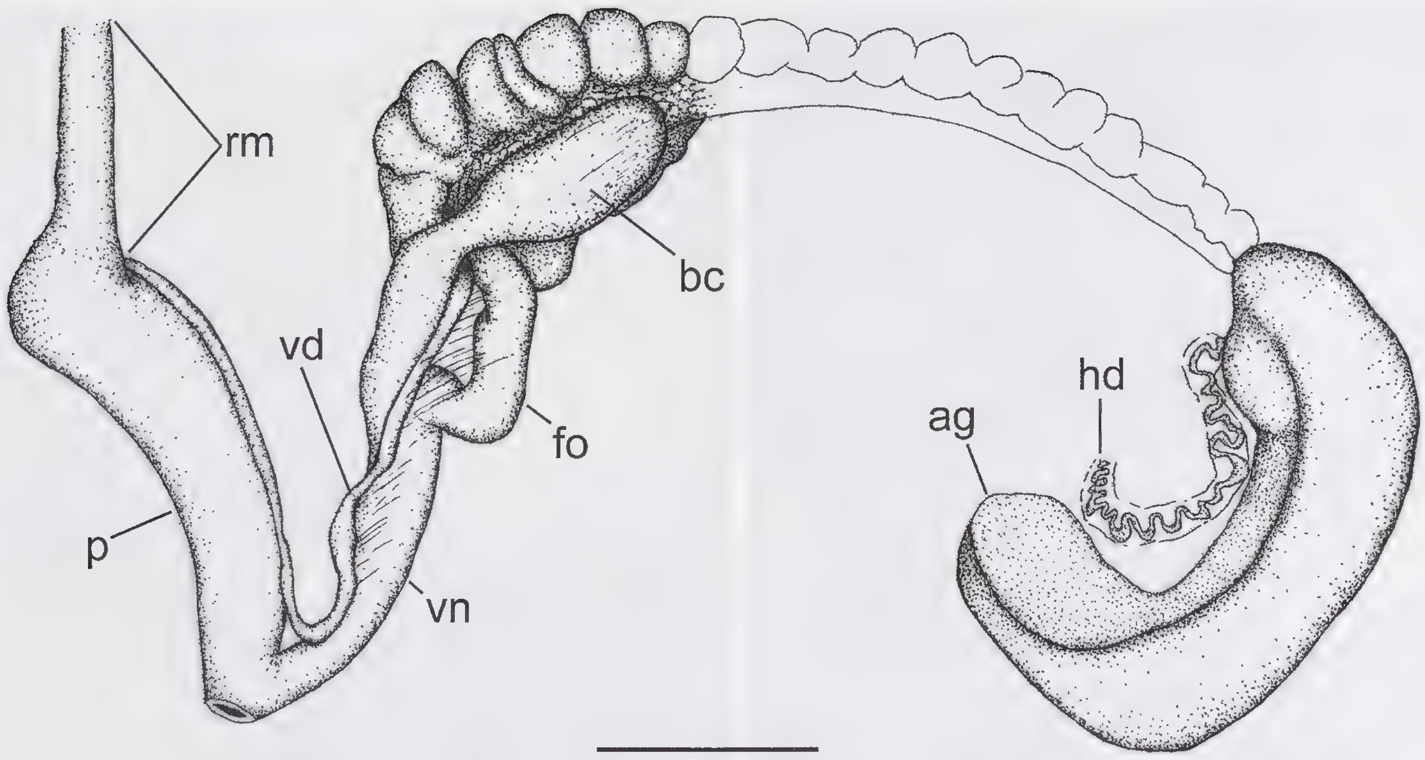

FIG. 73. Genital anatomy of ***Globorhagada wunandarra*** n. sp. holotype WAM S36635 (Boongaree Island, August). Schematic parts of spermoviduct reconstructed. Scale bar = 5 mm.

indistinct longitudinal pilaster may be present, lamellae or additional folds. Vagina long, bursa copulatrix wide, head well differentiated, inflated, connected to base of spermoviduct by connective tissue; free oviduct shorter than vagina, spermoviduct longer than anterior part of oviduct; albumen gland typical, large.

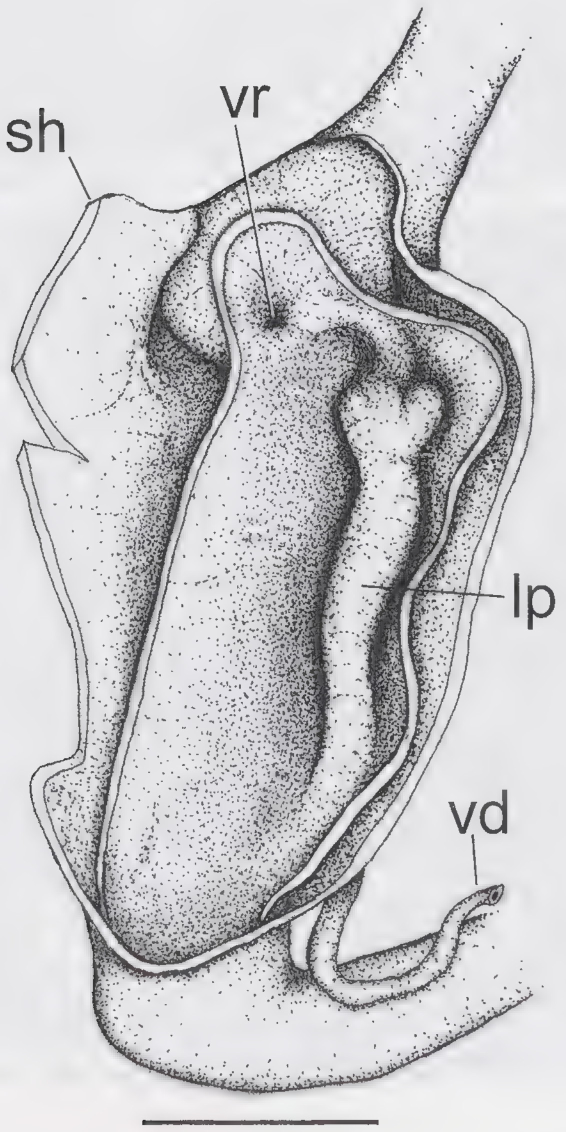

FIG. 74. Penial anatomy of ***Globorhagada wunandarra*** n. sp. holotype WAM S36635 (Boongaree Island, August). Scale bar = 3 mm.

Mitochondrial Differentiation

Mean infraspecific sequence divergence 0.004 (two sequences); mean p-distances to other species of the *G. ruberpumilio*-complex between 0.10 and 0.18; mean p-distances to species of the *G. prudhoensis*-complex 0.24–0.27.

Comparative Remarks

Shell typical of the *G. ruberpumilio*-complex, differing from *G. ruberpumilio* (from Youwanjela Creek, Prince Regent Reserve) and ***G. uwinsensis*** by more pronounced microsculpture on upper part of last teleoconch whorls and larger shell (D = 20.6–22.3 mm instead of 17.7–20.5 mm; as given by Solem, 1979; Table 4). In addition, penial wall lacking longitudinal folds and two flanking pilasters next to entrance of vas deferens near proximal end of interior surface of penial wall as reported for *G. ruberpumilio* by Solem (1979: fig. 6).

Distribution (Fig. 57)

Boongaree Island.

Globorhagada uwinsensis n. sp.

Figs. 58F, 75–77

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Hanover Bay, Uwins Island, 15°15'32"S, 124°48'08"E; col. Vince Kessner, 08/02/2009, KIS 3–130 (vine thicket, large fig trees on upper slopes, piles of sandstone rocks; active on ground after rain at night).

Material Examined

Holotype WAM S37626 (preserved specimen, dissected). Paratypes WAM S58485 (preserved specimen), AM C471862 (preserved animal, dissected), WAM S37627 (preserved specimen), WAM S36992–4 (3 preserved specimens), WAM S37085 (preserved specimen), AM C471863 (shell), WAM S37242–7 (17 shells) from Uwins Island.

Etymology

For Uwins Island, adjective.

Description

Shell (Figs. 58F, 75, Table 4): Very small for the genus, globose, with moderately elevated spire, last whorl extremely increased in height and diameter, accounting for two thirds of entire shell height, whorls well rounded below, slightly shouldered above slightly depressed at periphery; suture shallow. Protoconch 3.4 mm in diameter, about one whorl, smooth with only faint radial growth lines. Teleoconch with delicate axial growth lines, dense axial rows of microscopic pustules forming only immediately underneath suture on upper parts of penultimate and last whorl. Colour chestnut brown with beige to light brown suffusion at base of shell, outer lip colour may be darker than shell, inner lip purplish brown. Umbilicus partly concealed (0–40%).

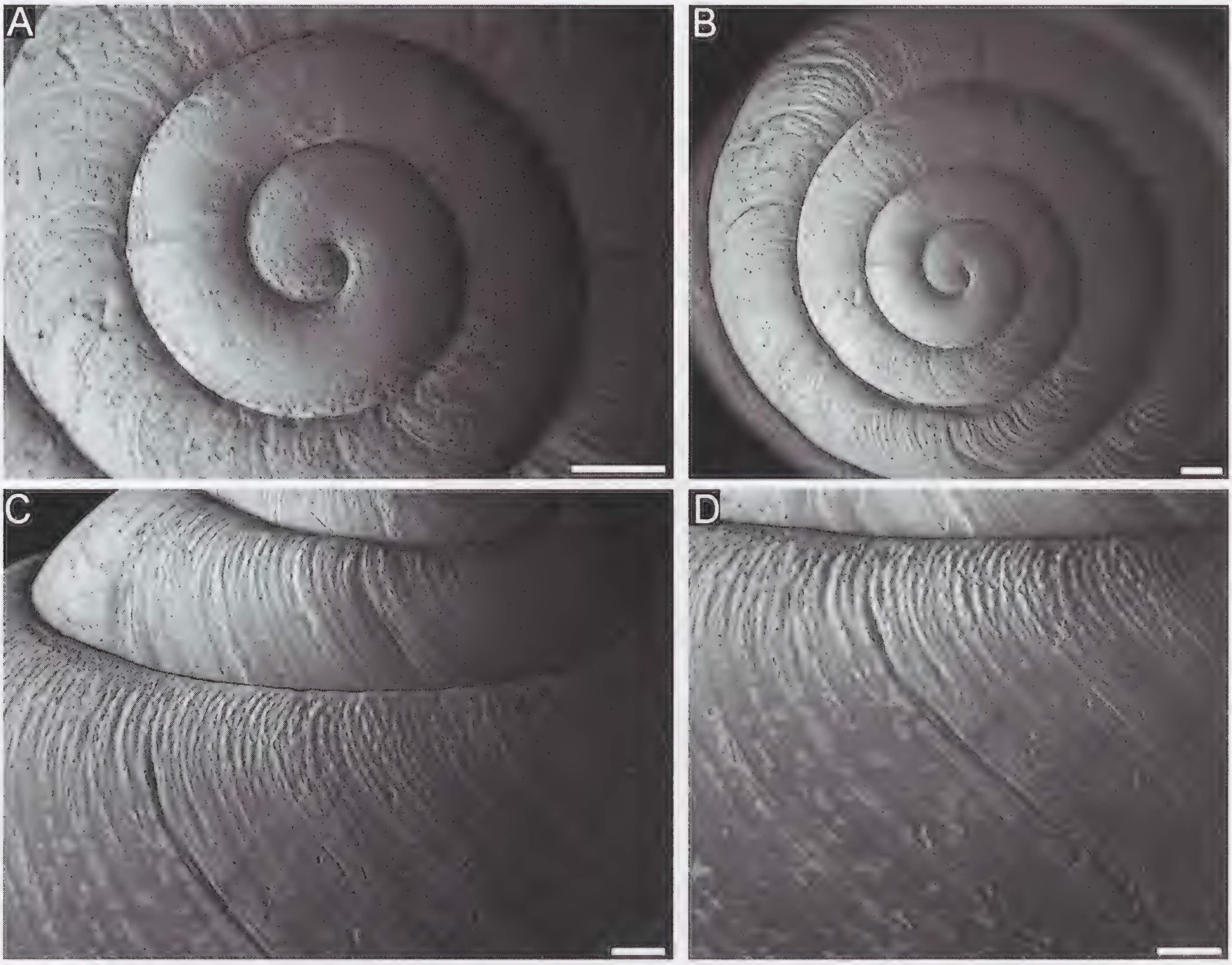

FIG. 75. SEM micrographs of the shell of ***Globorhagada uwinsensis*** n. sp. paratype AM C471863 (Uwins Island). A: Apical view showing protoconch; B: Apical view showing sculpture on first whorls; C: Lateral view showing sculpture on third and penultimate whorl; D: Close-up of sculpture on upper part of penultimate whorl. Scale bars = 1 mm.

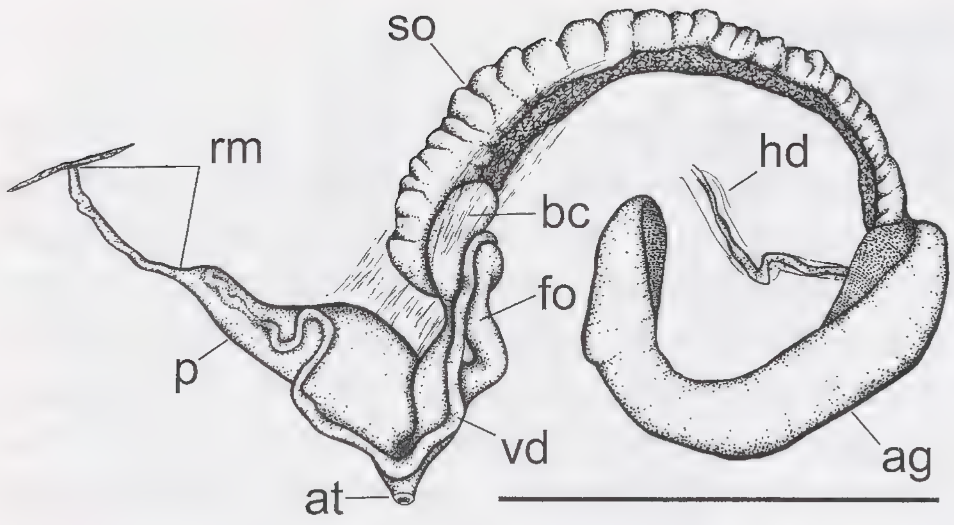

FIG. 76. Genital anatomy of ***Globorhagada uwinsensis*** n. sp. paratype AM C471862 (Uwins Island, February). Schematic parts of spermoviduct reconstructed. Scale bar = 5 mm.

Apertural lip well rounded, simple, flaring, sharp, nodes absent, parietal wall inconspicuous.

Genital anatomy (Figs. 76–77): Penis moderately long, bulbous, not coiled within penial sheath, with thick glandular walls. Vas entering penial sheath within distal third of penial complex, opening into penial lumen through simple vergic ring that gives rise to sperm gutter running along interior penial wall till proximal end; sperm gutter flanked by pad-like thickenings on each side, which support delicate, dense lateral lamellae; these lamellar pads extend to proximal end of penial wall, tapering in thickness. Vagina rather short, about as long as free oviduct. Bursa copulatrix wide, head inflated.

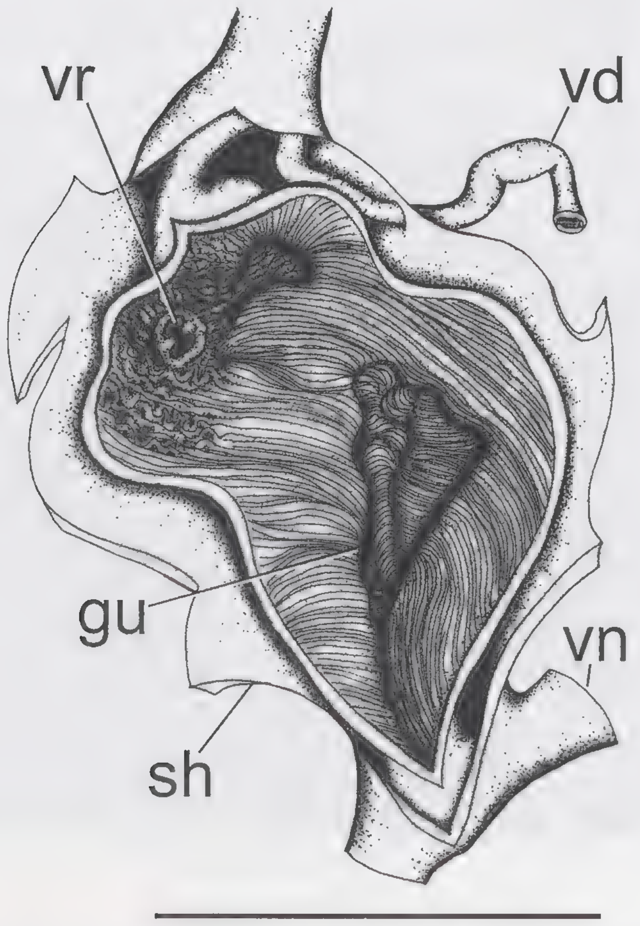

FIG. 77. Penial anatomy of ***Globorhagada uwinsensis*** n. sp. paratype AM C471862 (Uwins Island, February). Scale bar = 3 mm.

Comparative Remarks

Shell typical of *G. ruberpumilio* complex; smaller than ***G. wunandarra*** from Boongaree Island (Table 4), but of similar size as *G. ruberpumilio*; sculpture of microscopic pustulation much weaker than in ***G. wunandarra*** and found only immediately underneath suture. Penial anatomy differs by presence of lateral lamellae. Penial anatomy of *G. ruberpumilio* differs by presence of weak, irregular longitudinal pilasters.

Distribution (Fig. 57)

Uwins Island.

Rhagada Albers, 1860

Rhagada Albers, 1860 [in Martens & Albers]: 108–109; Pilsbry, 1890: 185–191; 1894: 135–136; Preston, 1908: 120; 1914: 13; Hedley, 1916: 69–70; Iredale, 1938: 112–113; 1939: 58–63; Solem, 1985a: 875–919; 1985b: 143–136; 1991: 217–218; 1997: 1663–1789; Solem & McKenzie, 1991: 247–263; Johnson & Black, 1991: 367–374; Withers et al., 1997: 599–611; Johnson et al., 2004: 341–355; 2006: 45–50; Maassen, 2009: 65–69. Type species: *Helix reinga* Pfeiffer, 1846, by original designation.

Bellrhagada Iredale, 1938: 114; Iredale, 1939: 71–72. Type species: *Rhagada plicata* Preston, 1914, by original designation.

Tumegada Iredale, 1939: 62. Type species: *Helix convicta* Cox, 1876, by original designation.

Taxonomic Remarks

The Western Australian species were revised by Solem (1985a, 1991, 1997), who also suggested synonymy of *Bellrhagada* and *Tumegada*. Maassen (2009) briefly revised the Indonesian *Rhagada* species known from Bali, Solor, Sumba, Flores and Alor.

Diagnosis

Shell: Small to medium sized (D = 9–25 mm; Table 5), thin to moderately thick, nearly flat to globose with moderately to strongly elevated, exceptionally also low spire; umbilicus frequently closed by greatly expanded callus, occasionally not fully concealed forming a chink; protoconch smooth to weakly sculptured by radial ridglets or ribs; teleoconch with faint to well-developed sculpture of irregular, axial ridgets or ribs, mostly

TABLE 5. Shell parameters of *Rhagada* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Height of First Whorl (FW)	Whorls	H/D Ratio
R. biggeana n. sp.	4	8.6–10.5 (9.9 ± 0.7)	13.7–15.3 (14.5 ± 0.8)	6.2–7.0 (6.6 ± 0.4)	4.6–4.8 (4.8 ± 0.1)	0.63–0.72 (0.68 ± 0.03)
R. sheaei n. sp.	18	10.6–14.3 (12.3 ± 0.9)	15.6–20.3 (17.9 ± 1.1)	7.1–9.0 (7.9 ± 0.5)	4.5–5.3 (4.9 ± 0.2)	0.61–0.76 (0.68 ± 0.03)
R. felicitas n. sp.	HT	8.8	13.1	6.0	5.25	0.67
	25	7.4–9.5 (8.3 ± 0.5)	11.5–14.3 (13.0 ± 0.7)	4.8–6.0 (5.4 ± 0.3)	4.2–5.0 (4.6 ± 0.2)	0.58–0.71 (0.64 ± 0.03)
R. cygna						
Sunday Is	6	7.0–8.2 (7.6 ± 0.4)	11.1–12.7 (11.9 ± 0.6)	5.1–5.6 (5.4 ± 0.2)	4.1–4.4 (4.2 ± 0.1)	0.60–0.68 (0.64 ± 0.03)
Hidden Is	16	7.6–9.2 (8.5 ± 0.5)	12.0–13.5 (12.7 ± 0.5)	5.4–6.2 (5.7 ± 0.2)	4.0–4.5 (4.3 ± 0.1)	0.61–0.73 (0.67 ± 0.04)
R. dominica n. sp.	HT	14.4	21.0	9.4	5.1	0.68
	24	11.0–14.9 (12.5 ± 0.8)	16.5–20.0 (18.3 ± 0.8)	7.7–9.0 (8.2 ± 0.4)	4.7–5.3 (5.5 ± 0.2)	0.62–0.82 (0.69 ± 0.05)
R. primigena n. sp.	HT	8.8	15.1	6.4	4.7	0.58
	18	8.5–10.0 (9.0 ± 0.4)	13.7–16.1 (14.8 ± 0.6)	5.8–6.7 (6.2 ± 0.3)	4.4–4.7 (4.5 ± 0.0)	0.56–0.69 (0.61 ± 0.03)

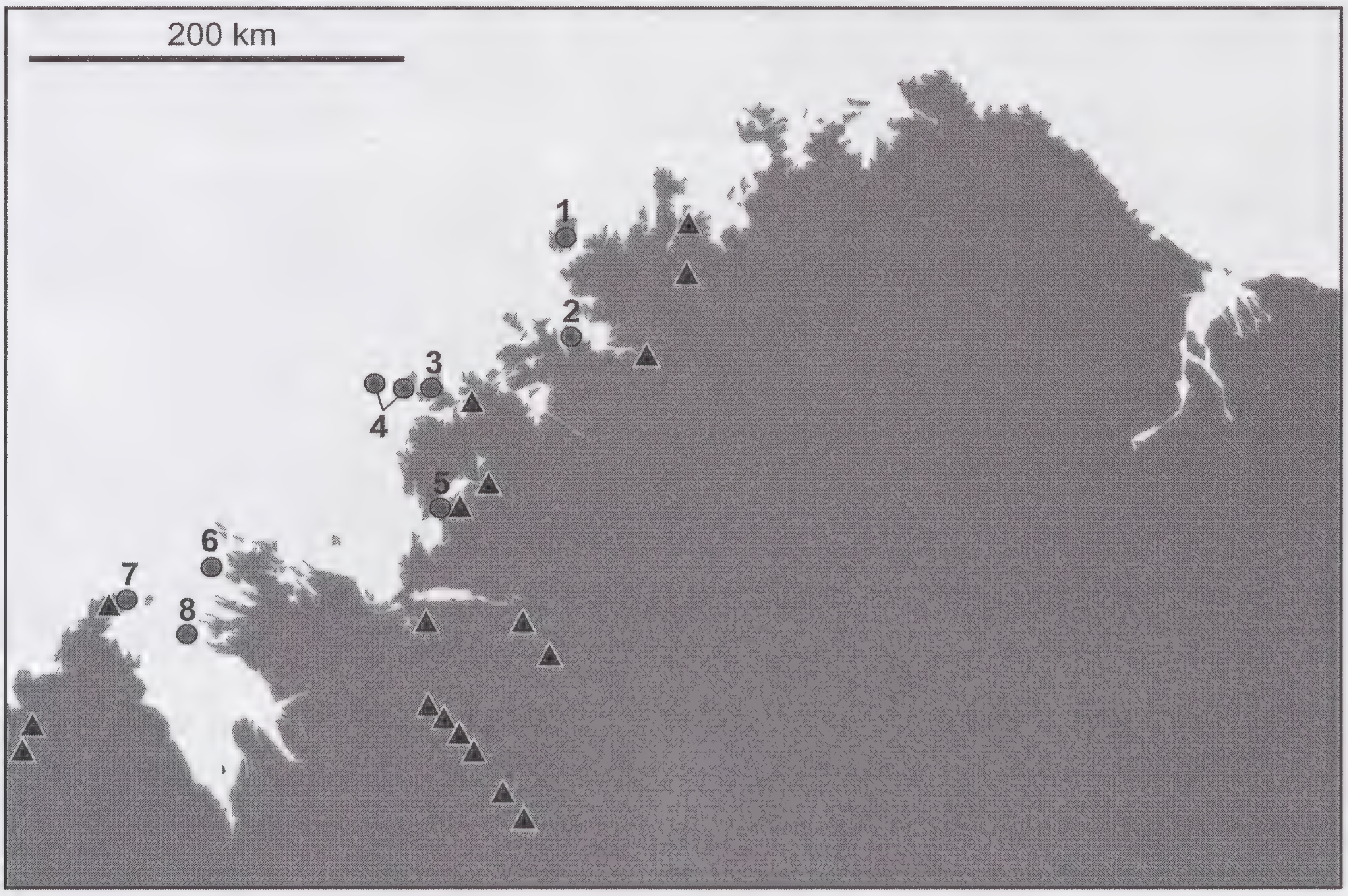

FIG. 78. Distribution map of *Rhagada*. Circles = records of species treated herein: 1: ***R. biggeana*** (Bigge Island), 2: *Rhagada* sp. (Boongaree Island), 3: ***R. kessneri*** (NW Augustus Island), 4: ***R. sheaei*** (Byam Martin and Chamapgny Islands), 5: ***R. felicitas*** (Storr Island), 6: *R. cygna* (Hidden Island), 7: *R. cygna*, ***R. dominica*** (Sunday Island), 8: ***R. primigena*** (Long Island); triangles = records of various species listed by Solem (1991).

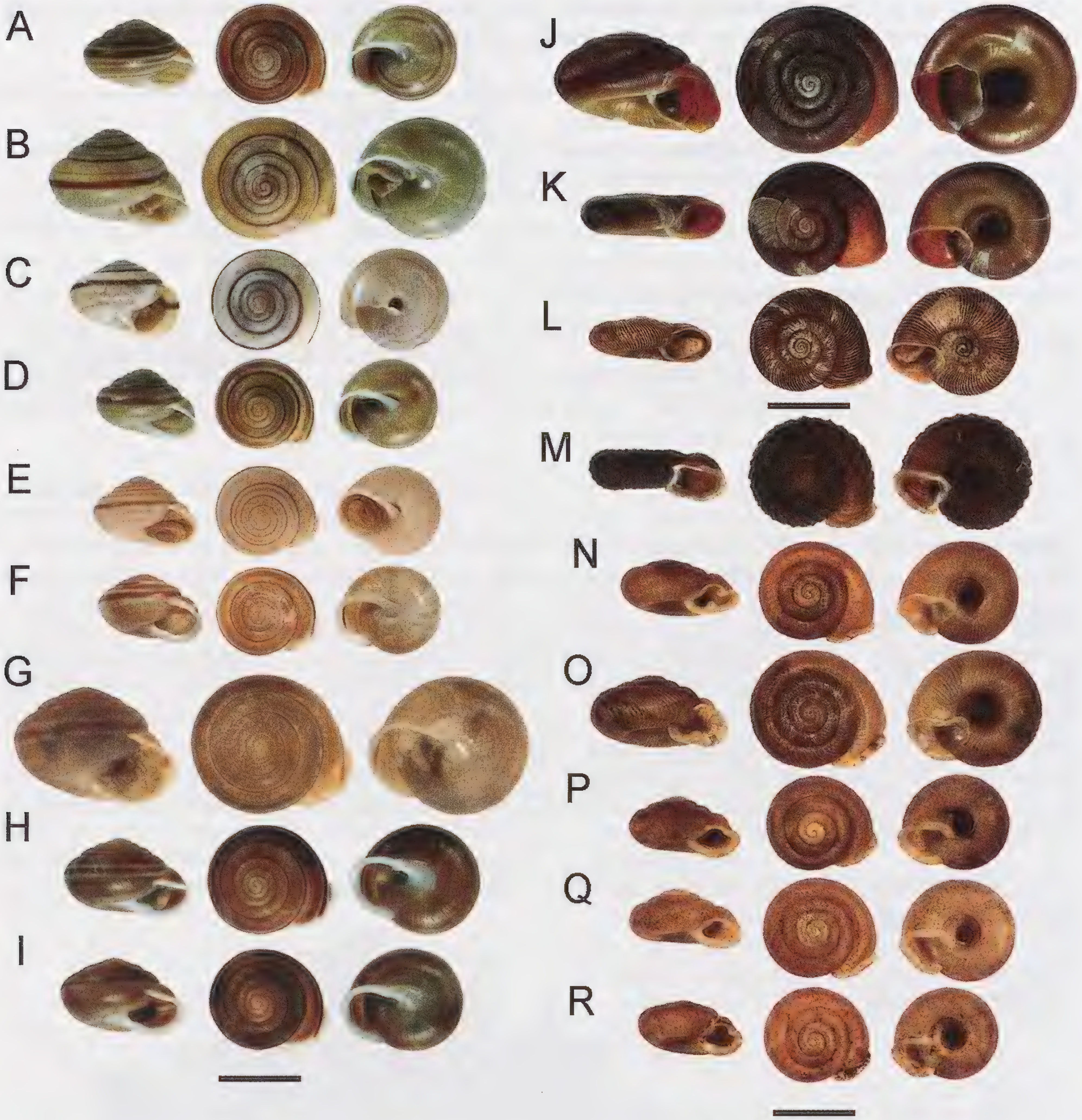

FIG. 79. Shells of *Rhagada*, *Retroterra*, **Molema** and *Baudinella*. A: ***Rhagada biggeana*** n. sp. paratype WAM S58486 (Bigge Island); B: ***Rhagada sheaei*** n. sp. paratype WAM S37074 (Byam Martin Island); C: ***R. sheaei*** n. sp. WAM S37693 (subadult, Champagny Island); D: ***Rhagada felicitas*** n. sp. holotype WAM S58487 (Storr Island); E: *Rhagada cygna* WAM S37728 (Hidden Island); F: *R. cygna* WAM S37831 (Sunday Island); G: ***Rhagada dominica*** n. sp. holotype WAM S58488 (Sunday Island); H: ***Rhagada primigena*** n. sp. holotype WAM S37721 (Long Island); I: ***R. primigena*** n. sp. paratype WAM S37719 (Long Island); J: ***Retroterra aequabilis*** n. sp. holotype WAM S58448 (Boongaree Island); K: ***Retroterra discoidea*** n. sp. holotype WAM S58449 (Uwins Island); L: ***Retroterra acutocostata*** n. sp. paratype WAM S37644 (1.3 km S of Halfway Bay); M: ***Molema stankowskii*** n. sp. holotype WAM S58447 (Molema Island). N: ***Baudinella thielei*** n. sp. paratype WAM S36975 (Bigge Island); O: ***Baudinella boongareensis*** n. sp. paratype WAM S37686 (Boongaree Island); P: ***Baudinella tuberculata*** n. sp. paratype WAM S37259 (Coronation Island); Q: ***Baudinella setobaudinioides*** n. sp. paratype WAM S37267 (Augustus Island); R: ***Baudinella occidentalis*** n. sp. paratype WAM S49043 (D'Arcy Island). Scale bars A–L = 10 mm; M–R = 20 mm. Note that foot protrudes from some shells.

on upper sector of whorls, with underlying vague calcareous undulations; whorls moderately increasing, separated by shallow to flat suture; periphery well rounded to weakly angulated. Shell colour variable, banded, background often whitish or brownish horn, with well-developed, red subsutural, supra-peripheral and frequently additional, thinner spiral bands. Head with eversible head wart opening between and just posterior to ommatophores.

Genital anatomy: Penis without penial sheath, embedded into connective tissue, with well-developed, long and coiled epiphallus that supports an epiphallic flagellum of variable length. Penial retractor muscle attached at epiphallus. Epiphallus opens to lumen of

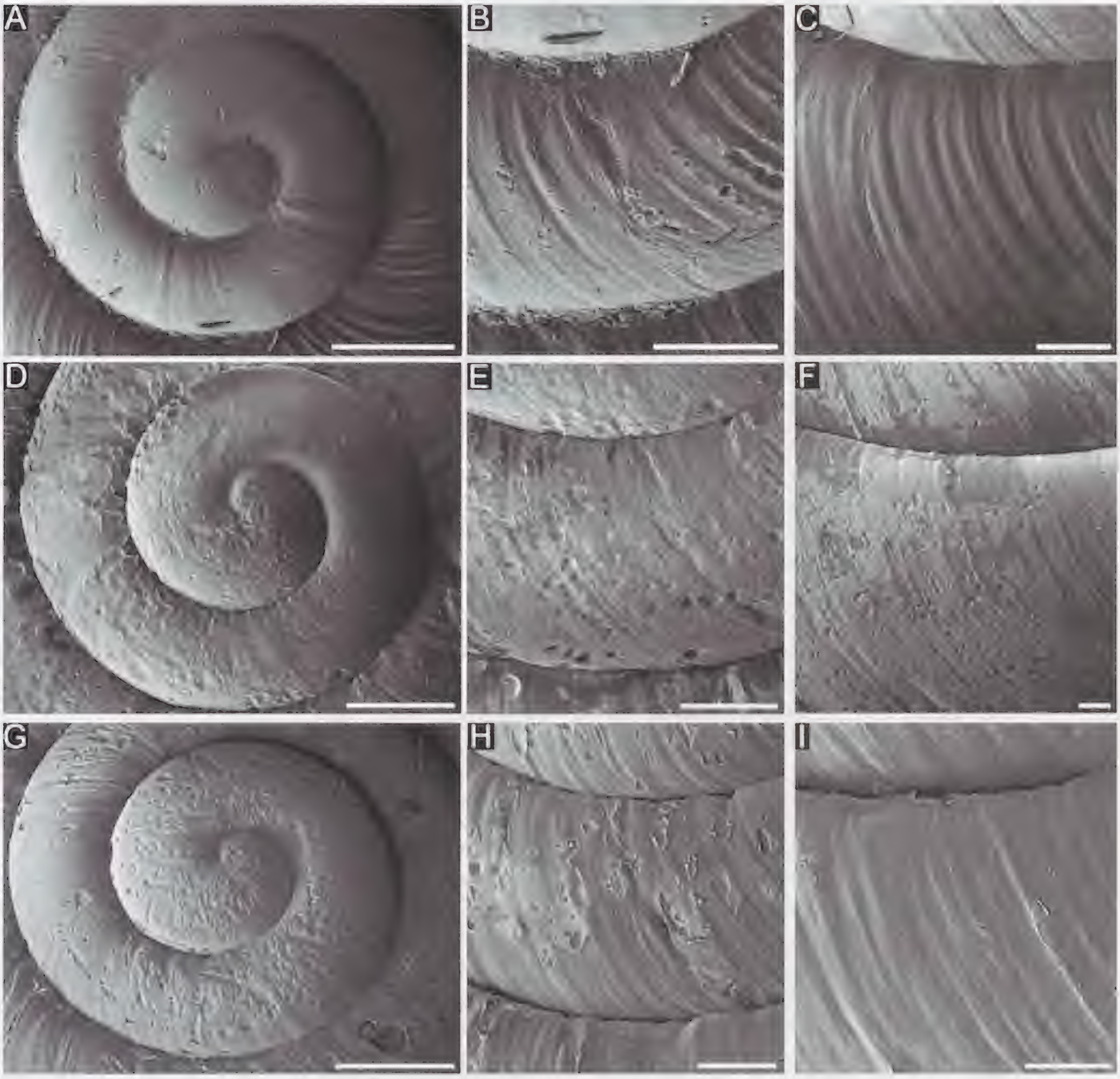

FIG. 80. SEM micrographs of shells of *Rhagada* species. A–C: ***Rhagada biggeana*** n. sp. paratype AM C471865 (Bigge Island). A: Apical view showing protoconch; B: Close-up of sculpture on second to third whorl; C: Close-up of sculpture on last whorl; D–F: ***Rhagada sheaei*** n. sp. paratype AM C471867 (Byam Martin Island). D: Apical view showing protoconch; E: Close-up of sculpture on second to third whorl; F: Close-up of sculpture on last whorl; G–I: ***Rhagada felicitas*** n. sp. paratype AM C471870 (Storr Island). G: Apical view showing protoconch; H: Close-up of sculpture on second to third whorl; I: Close-up of sculpture on last whorl. Scale bars: A, D, G = 1 mm; B–C, E–F, H–I = 500 µm.

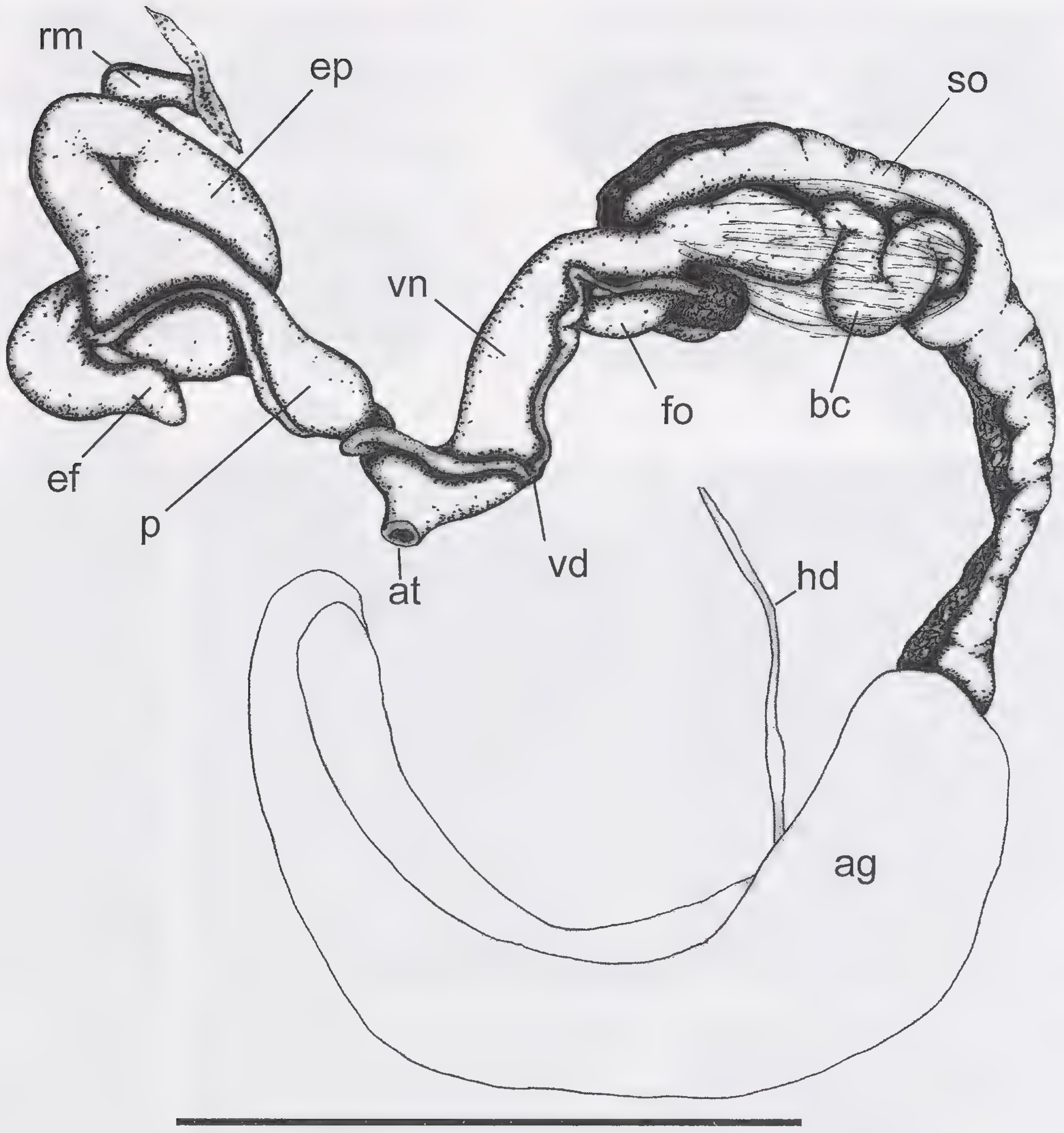

FIG. 81. Genital anatomy of ***Rhagada biggeana*** n. sp. holotype WAM S36739 (Bigge Island, August). Scale bar = 10 mm.

penial chamber through large, cone-shaped verge with characteristic sperm groove running down from opening of channel at tip of verge. Bursa copulatrix short to long, simple to kinked.

Aestivation Strategy

Free sealer (modified after Solem, 1997).

Diversity and distribution (Fig. 78)

Widespread in coastal regions of Western Australia between Shark Bay and Mitchell Plateau. In Indonesia, known from some of the Smaller Sunda Islands; likely widespread between Timor and Bali. Solem's (1997) statement that *Rhagada* is an Australian endemic is refuted based on molecular evidence (Köhler, unpubl. data). Twenty-six species currently known from Western Australia; six additional species described herein. Dry and worn shells found on Boongaree Island do not permit identification but are thought to represent a further undescribed species (WAM S36043).

Rhagada biggeana n. sp.

Figs. 79A, 80A–C, 81, 82

Type Locality

Northwestern Kimberley, Bonaparte Archipelago, W coast of Bigge Island, 9.15 km NW of Savage Hill, 14°34'59"S, 125°06'22"E; coll. Michael Shea, 3/08/2007, KIS 1–19 (low open woodland, sandstone over laterite).

Material Examined

Holotype WAM S36739 (preserved specimen, dissected). Paratypes WAM S58486 (preserved specimen), AM C471864 (shell), AM C471865 (2 shells), WAM S36042 (5 shells) from type locality; WAM S36040 (7 shells) from 14°35'14"S, 125°11'08"E; WAM S36041 (3 shells) from 14°35'06"S, 125°06'12"E.

Etymology

For Bigge Island, adjective of female gender.

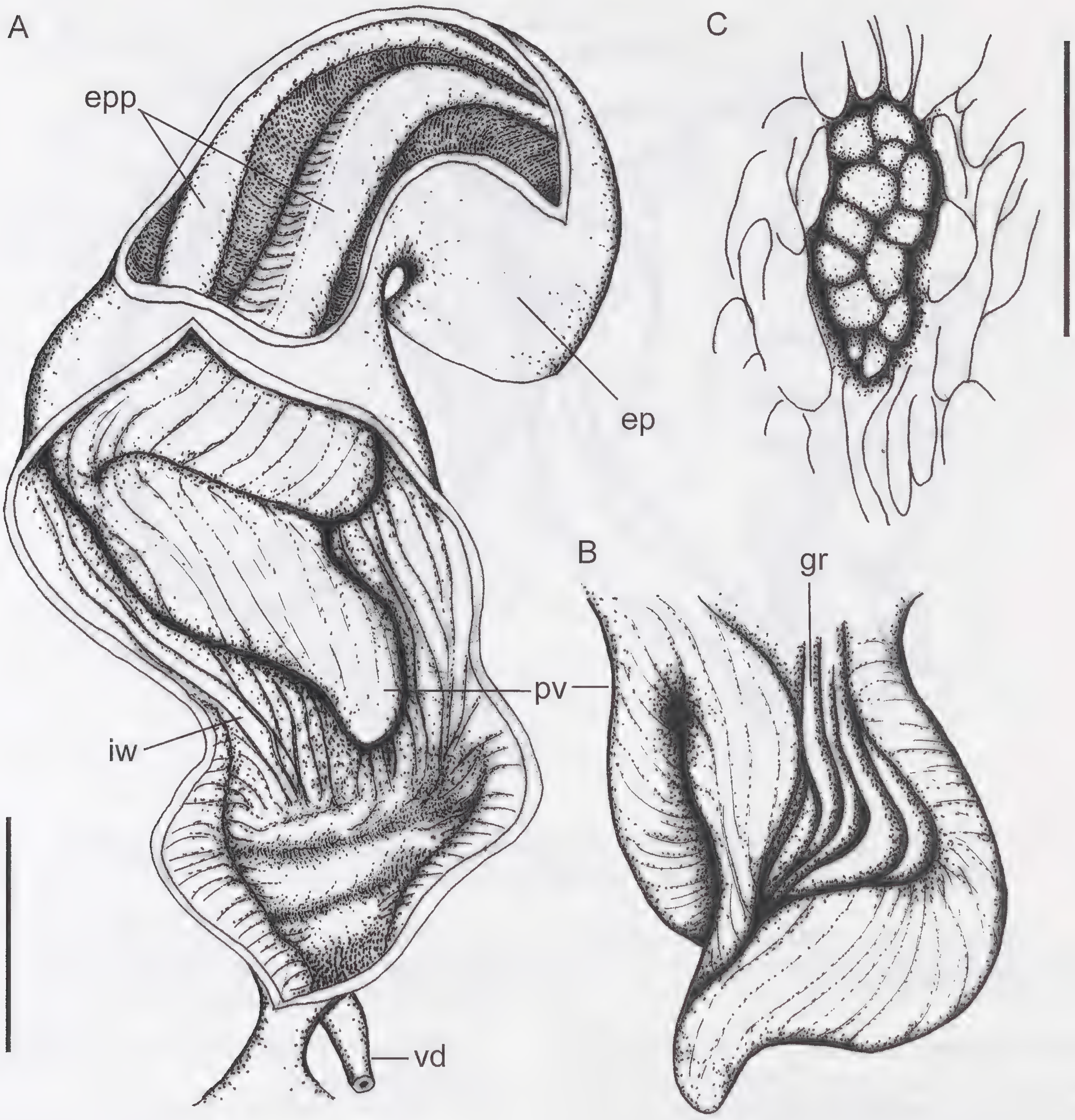

FIG. 82. Penial anatomy and head wart of ***Rhagada biggeana*** n. sp. holotype WAM S36739 (Bigge Island, August). A: Penial anatomy. Scale bar = 3 mm; B: Magnification of backside of penial verge; C: Head wart. Scale bar = 1 mm.

Description

Shell (Figs. 79A, 80A–C, Table 5): Small to moderate in size, thin to solid, broadly conical with moderately to conspicuously elevated spire; periphery well rounded to slightly depressed; last whorl well rounded above and below periphery; umbilicus closed (~ 2/3 of adults) or forming a chink (~ 1/3 of adults); background colour white; supra-peripheral band varying in development, usually well developed, rather thin to moderately thick, distinct, visible on all to most whorls; subsutural and additional spiral bands vary in number and development, thinner and lighter in colour. Protoconch ~ 2.6 mm in diameter, 1.5 whorls, smooth. Teleoconch smooth with faint radial growth lines. Angle of aperture ~ 45°; last whorl abruptly descending behind lip; outer lip rounded, sharp to thin, slightly expanded, basal node of lip weak, palatal node absent.

Genital anatomy and *head wart* (Figs. 81–82): Penis short, with slightly inflated proper and long, coiled epiphallus; distal two thirds of inner penial wall with weak longitudinal ridges, proximal third rather smooth; inner epiphallic wall with two well-developed longitudinal pilasters; penial verge large, conical, with pointed tip, extending more than half of length of penial chamber, kinked, smooth, groove supporting fine longitudinal lamellae. Head wart small, elongate-ovate (Fig. 82C).

Mitochondrial Differentiation

One specimen sequenced (holotype); interspecific genetic distances: 0.11 with regard to ***R. kessneri***, 0.20–0.22 to all other congeners.

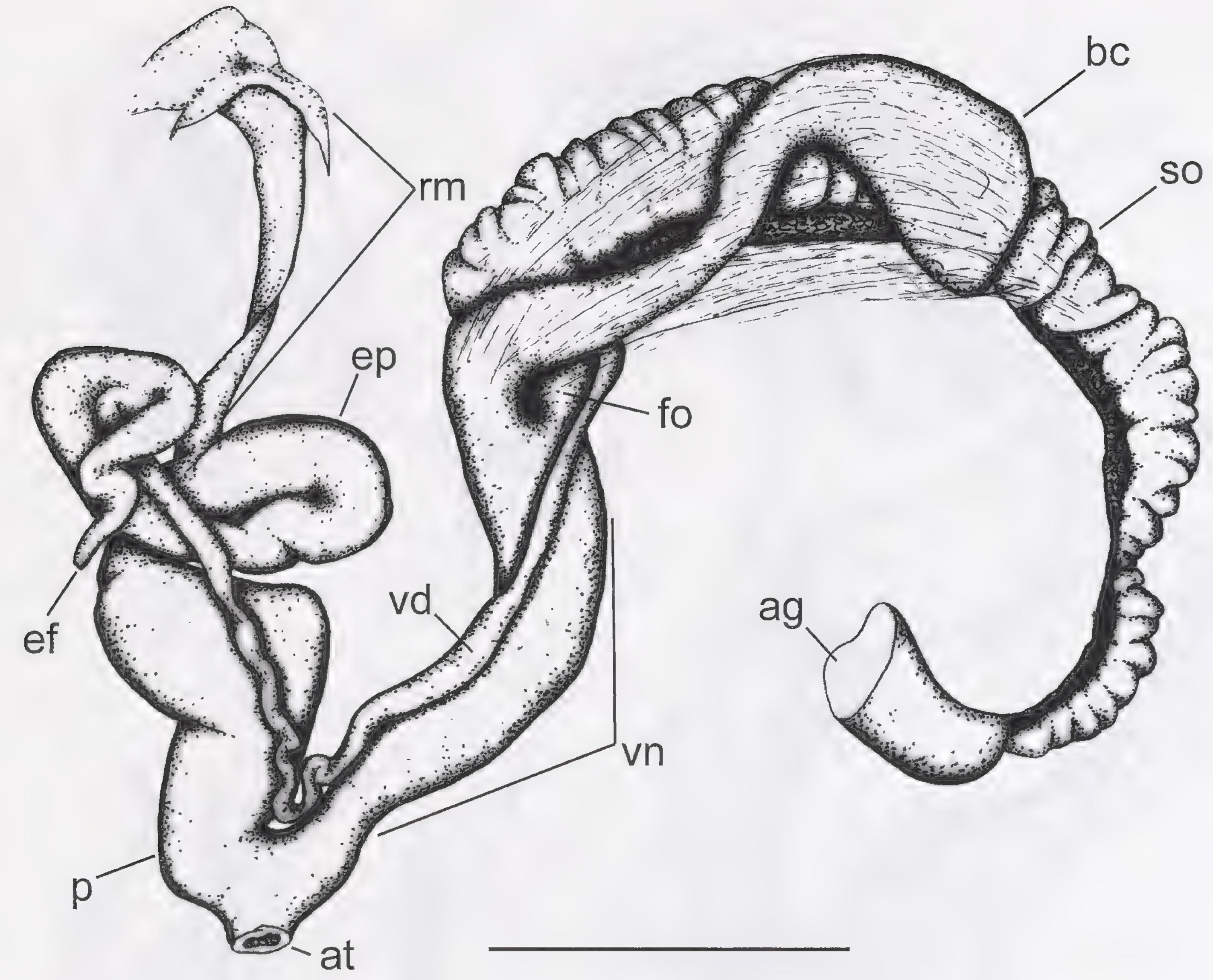

FIG. 83. Genital anatomy of ***Rhagada kessneri*** n. sp. holotype WAM S37678 (Augustus Island, February). Scale bar = 5 mm.

Comparative Remarks

Description based on worn or leached shells plus dissection of holotype. Genetic distances support status as distinct species with respect to all other congeners studied herein. Similarly, ***R. kessneri*** from Augustus Island has a large, conical verge and well-developed longitudinal epiphallic pilasters but differs by weaker sculpture of inner penial wall, and rounded shape of head wart. Present species identical with "*Rhagada* species 1" listed by Solem (1991).

Distribution (Fig. 78)

Bigge Island.

Rhagada kessneri n. sp.

Figs. 83, 84

Type Locality

Central Kimberley coast, Bonaparte Archipelago, Camden Sound, NW section of Augustus Island, 15°20'11"S, 124°31'10"E; coll. Vince Kessner, 13/02/2009, KIS 1–67 (open woodland on moderately steep W-facing slopes at the base of sandstone cliffs).

Material Examined

Holotype WAM S37678 (preserved specimen, dissected).

Etymology

Named in honour of Vince Kessner (Adelaide River), in recognition of his most valuable contributions to successful implementation of the Kimberley Island Survey; noun in genitive case.

Description

Genital anatomy and *head wart* (Figs. 83–84): Penis moderately long, with slightly inflated proper and long, coiled epiphallus, well-developed epiphallic flagellum; penial wall thick proximally, thin distally, interiorly rather smooth with weak longitudinal folds at proximal end; inner epiphallic wall with one well-developed longitudinal pilaster; penial verge large, conical, with pointed tip, extending more than half of length of penial chamber, smooth with simple groove. Vagina strongly elongated; free part of oviduct very short, coiled; bursa copulatrix long, considerably extending anterior end of spermoviduct, connected to base of spermoviduct by connective tissue, head clearly

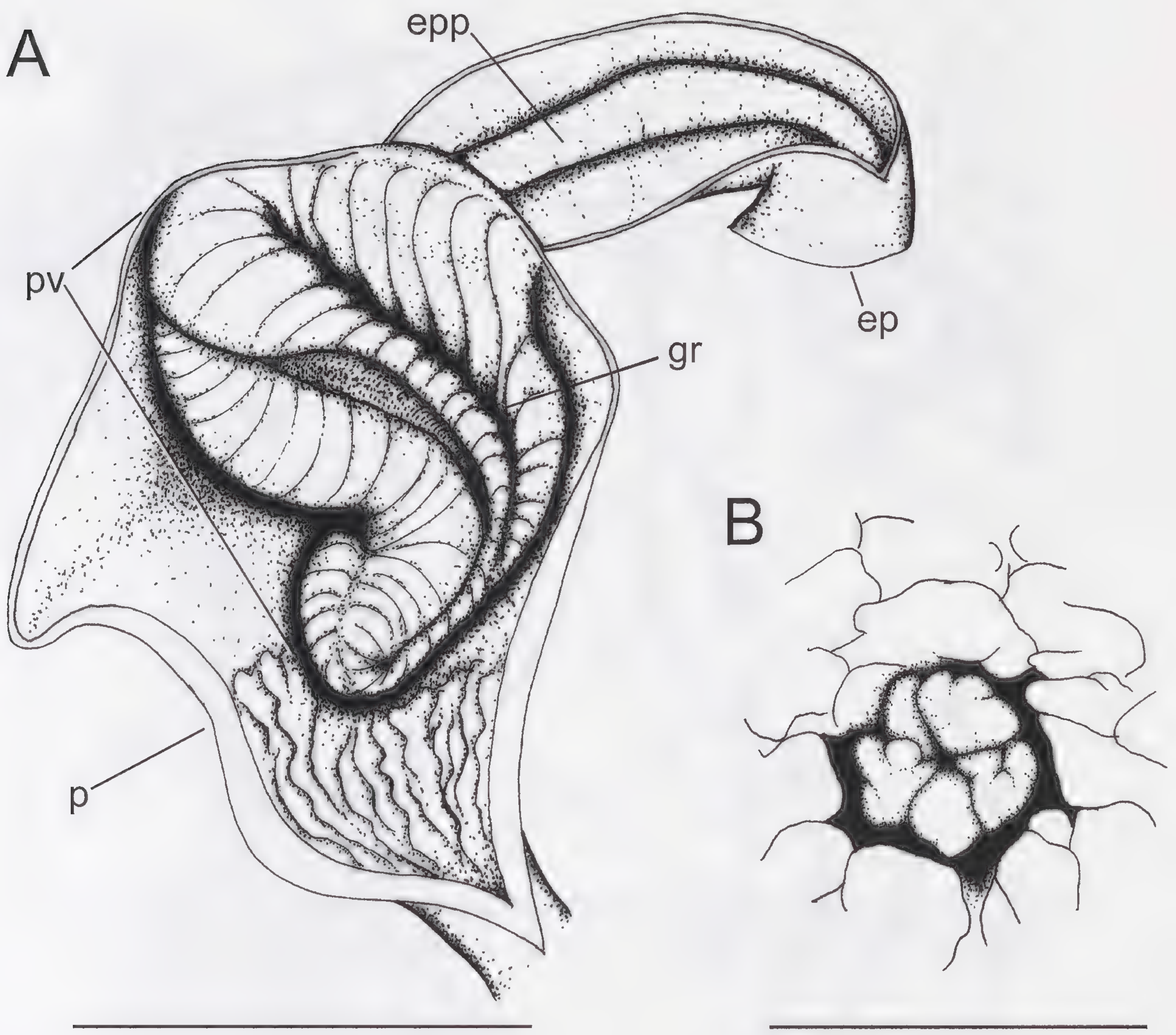

FIG. 84. Penial anatomy and head wart of ***Rhagada kessneri*** n. sp. holotype WAM S37678 (Augustus Island, February). A: Penial anatomy. Scale bar = 3 mm; B: Head wart. Scale bar = 1 mm.

differentiated, not kinked, inflated. Head wart small, round (Fig. 84C).

Mitochondrial Differentiation

One specimen sequenced (holotype); interspecific genetic distances: 0.11 to ***R. biggeana***, 0.20–0.21 to all other congeners.

Comparative Remarks

Description based on dissection of one specimen with cracked shell. Genetic distances support distinct status with respect to all other congeners studied herein. ***R. biggeana*** is most similar for its large, conical verge and well-developed longitudinal epiphallic pilasters but differs by stronger sculpture of inner penial wall, having two instead of one epiphallic pilasters, more complex sperm groove of penial verge, elongate head wart.

Distribution (Fig. 78)

Known from northwestern Augustus Island only.

Rhagada sheaei n. sp.

Figs. 79B–C, 80D–F, 85, 86

Type Locality

Central Kimberley coast, Bonaparte Archipelago, Camden Sound, Byam Martin Island, 15°23'09"S, 124°21'42"E; coll. Michael Shea, 3/06/2009, KIS 1–61 (dry vine thicket patches, and eucalypts on S-facing slope, on sandstone).

Material Examined

Holotype WAM S37074 (dissected specimen). Paratypes WAM S49019 (shell) from type locality; WAM S37679 (preserved specimen), AM C471866 (7 shells), AM C471867 (shell), WAM S37302 (20 shells) from 15°23'10.6"S, 124°21'42.3"E. Additional non-type material WAM S37693 (preserved specimen) from Champagny Island, 15°18'26"S, 124°16'58"E.

Etymology

Named in honour of Michael Shea (Sydney), who collected some of the types.

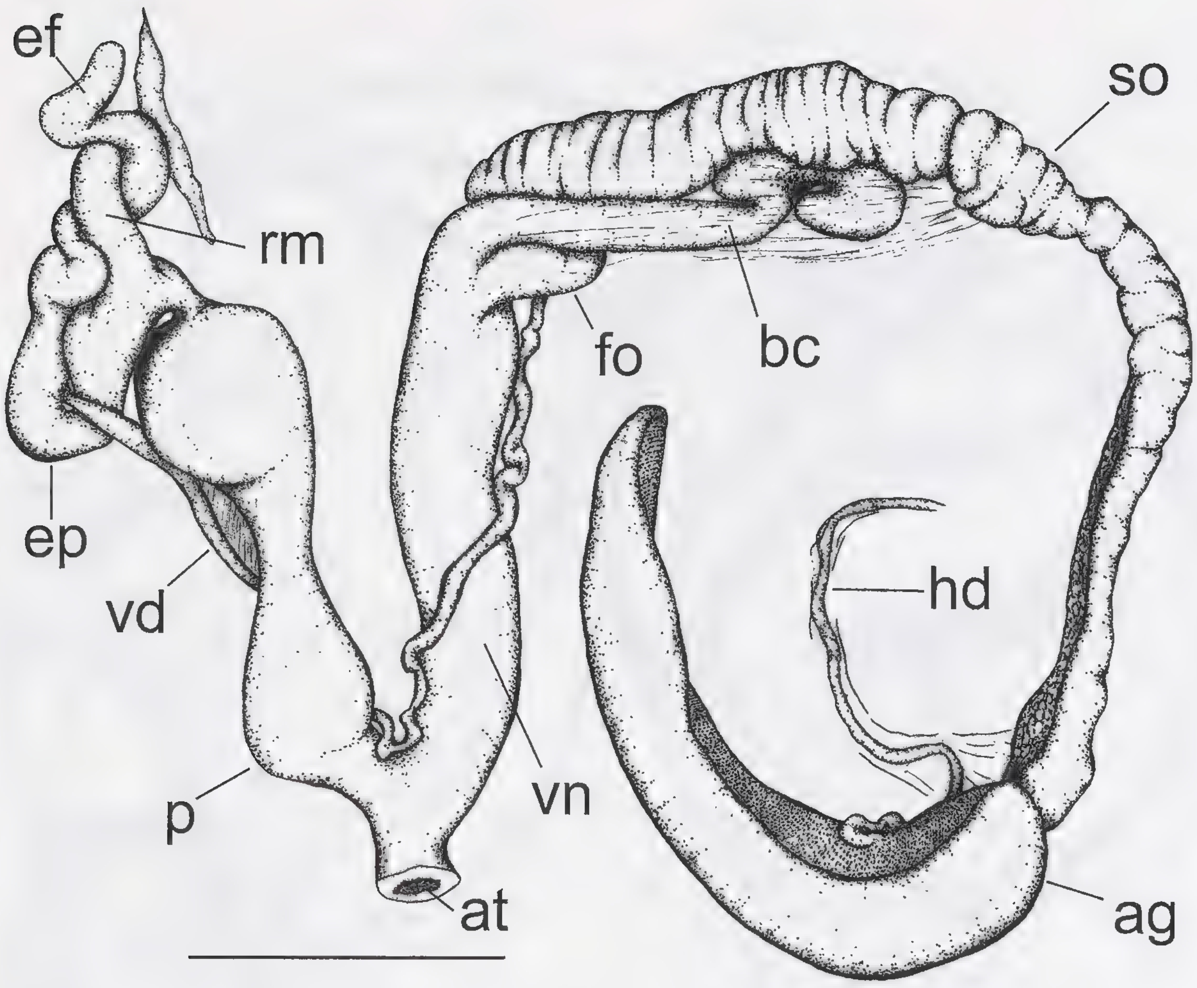

FIG. 85. Genital anatomy of ***Rhagada sheaei*** n. sp. holotype WAM S37074 (Byam Martin Island, June). Scale bar = 5 mm.

Description

Shell (Figs. Figs. 79B, C, 80D–F, Table 5): Moderate in size (comparatively large for genus), solid, broadly conical with strongly elevated spire; periphery slightly depressed to slightly angulated; last whorl well rounded above and below periphery; umbilicus closed (~ 2/3 of adults) or forming a chink (~ 1/3 of adults); background colour white, sometimes with reddish brown suffusion at upper whorls; supra-peripheral band usually strongly developed, moderately thick, distinct, visible on all or most whorls; subsutural band varies from absent to thick, additional spiral bands thinner and lighter in colour, varying in number from one to three above, nil to seven below supra-peripheral band, in development from diffuse to distinct. Protoconch ~ 3 mm in diameter, with 1.5–2 whorls, smooth. Teleoconch smooth with faint radial growth lines. Angle of aperture ~ 45°; last whorl abruptly descending behind lip; outer lip rounded, slightly expanded, basal node of lip weak, palatal node absent.

Genital anatomy and *head wart* (Figs. 85–86): Penis moderately long, proximally and distally inflated with moderately long, coiled epiphallus, well-developed epiphallic flagellum; penial wall thick proximally, thin distally, interiorly smooth with faint oblique (distal) to longitudinal (proximal) folds and few weak longitudinal pilasters at proximal end; inner epiphallic wall with many fine longitudinal pilasters; penial verge large, conical, with pointed tip, extending more than half of length of penial chamber, smooth with simple groove. Vagina strongly elongated; free part of oviduct very short, coiled; bursa copulatrix long, considerably extending anterior end of spermoviduct, connected to base of spermoviduct by connective tissue, head clearly differentiated, coiled or kinked, slightly inflated. Head wart small, irregularly shaped (Fig. 86C).

Mitochondrial Differentiation

Three specimens sequenced; infraspecific genetic distance 0.01 (on Byam Martin Island)–0.03 (between islands); interspecific genetic distance: 0.20–0.24 all other congeners.

Comparative Remarks

Description based on dissection of one specimen. Genetic distances support status as distinct species with respect to all other congeners studied herein. Shell larger than ***R. biggeana*** (Table 5); differs from ***R. biggeana*** and ***R. kessneri*** by number and development of epiphallic pilasters, kinked head of bursa copulatrix and different shape of head wart.

Distribution (Fig. 78)

Byam Martin and Champagny islands, Heywood Island group.

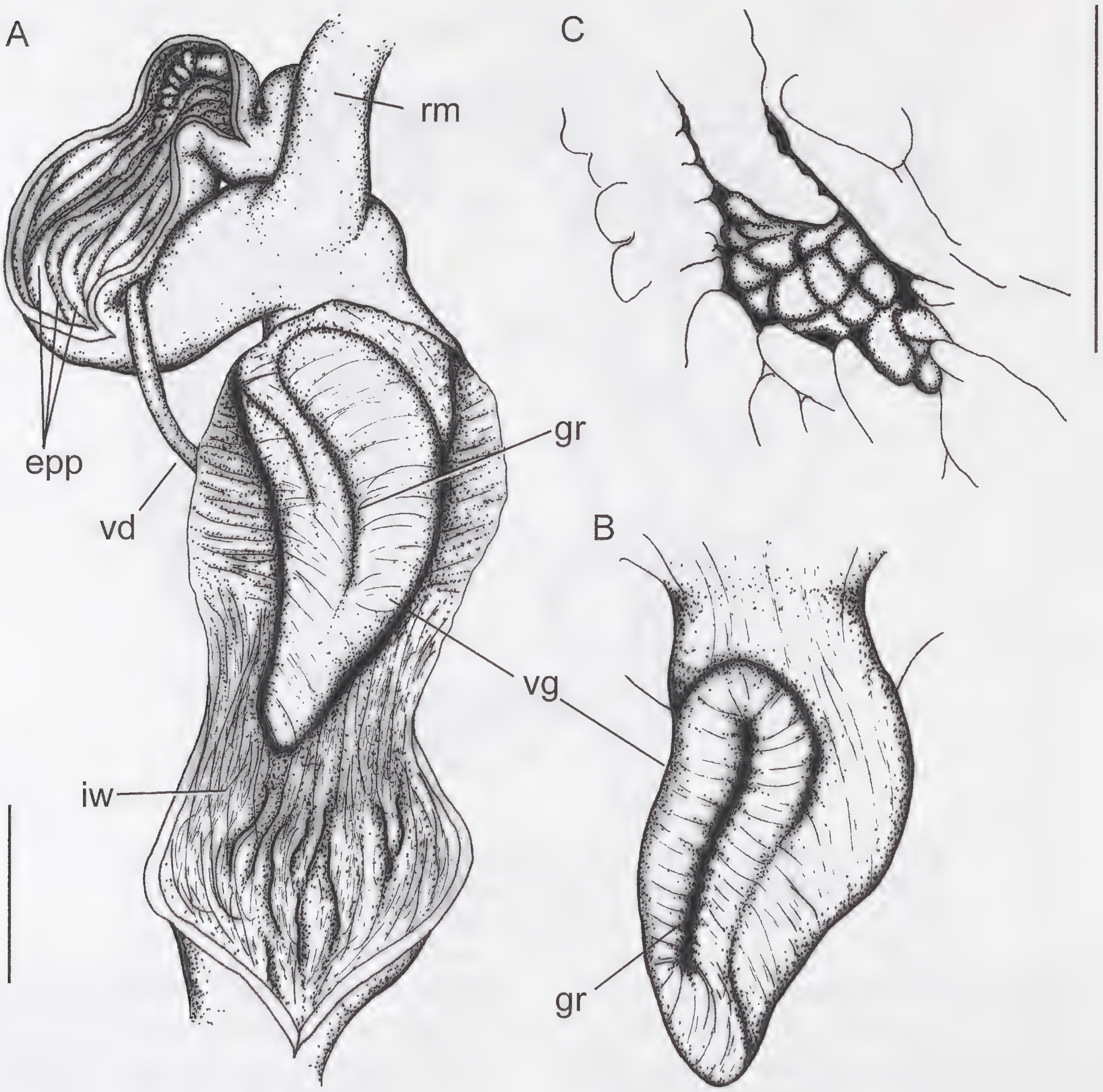

FIG. 86. Penial anatomy and head wart of ***Rhagada sheaei*** n. sp. holotype WAM S37074 (Byam Martin Island, June). A: Penial anatomy; B: Magnification of backside of penial verge; C: Head wart. Scale bars = 1 mm.

Rhagada felicitas n. sp.

Figs. 79D, 80G–I, 87, 88

Type Locality

Western Australia, southwestern Kimberley, Doubtful Bay, southeastern section of Storr Island, 15°56'58"S, 124°33'24"E; coll. Vince Kessner, 21/05/2009, KIS 3–140 (in soil under rocks around roots of baobab tree on flat and open sandstone platform with talus and patches of *Spinifex*-grass).

Material Examined

Holotype WAM S58487 (preserved specimen). Paratypes AM C471868 (5 preserved specimens), WAM S37724 (14 preserved specimens), AM C471869 (15 shells), WAM S37838 (27 shells) from type locality; WAM S37722 (7 preserved specimens), WAM S37723 (7 preserved specimens), WAM S37725 (3 preserved specimens), WAM S37726 (3 preserved specimens), WAM S37727 (6 preserved specimens), AM C471870 (shell), WAM S37834 (4 shells), WAM S37835 (4 shells), WAM S37836 (4 shells), WAM S37837 (13 shells), WAM S37839 (4 shells), WAM S37840 (4 shells), WAM S37841 (3 shells) from southeastern section of Storr Island, 15°56'58"–57'40"S, 124°33'18–38"E.

Etymology

From "*felicitas*" (Latin = success, but also happiness) in reference to the name of Success Strait, north of Storr Island; noun in apposition.

Description

Shell (Figs. 79D, 80G–I, Table 5): Small, thin but solid, broadly conical with depressed spire; periphery well rounded to slightly angulated;

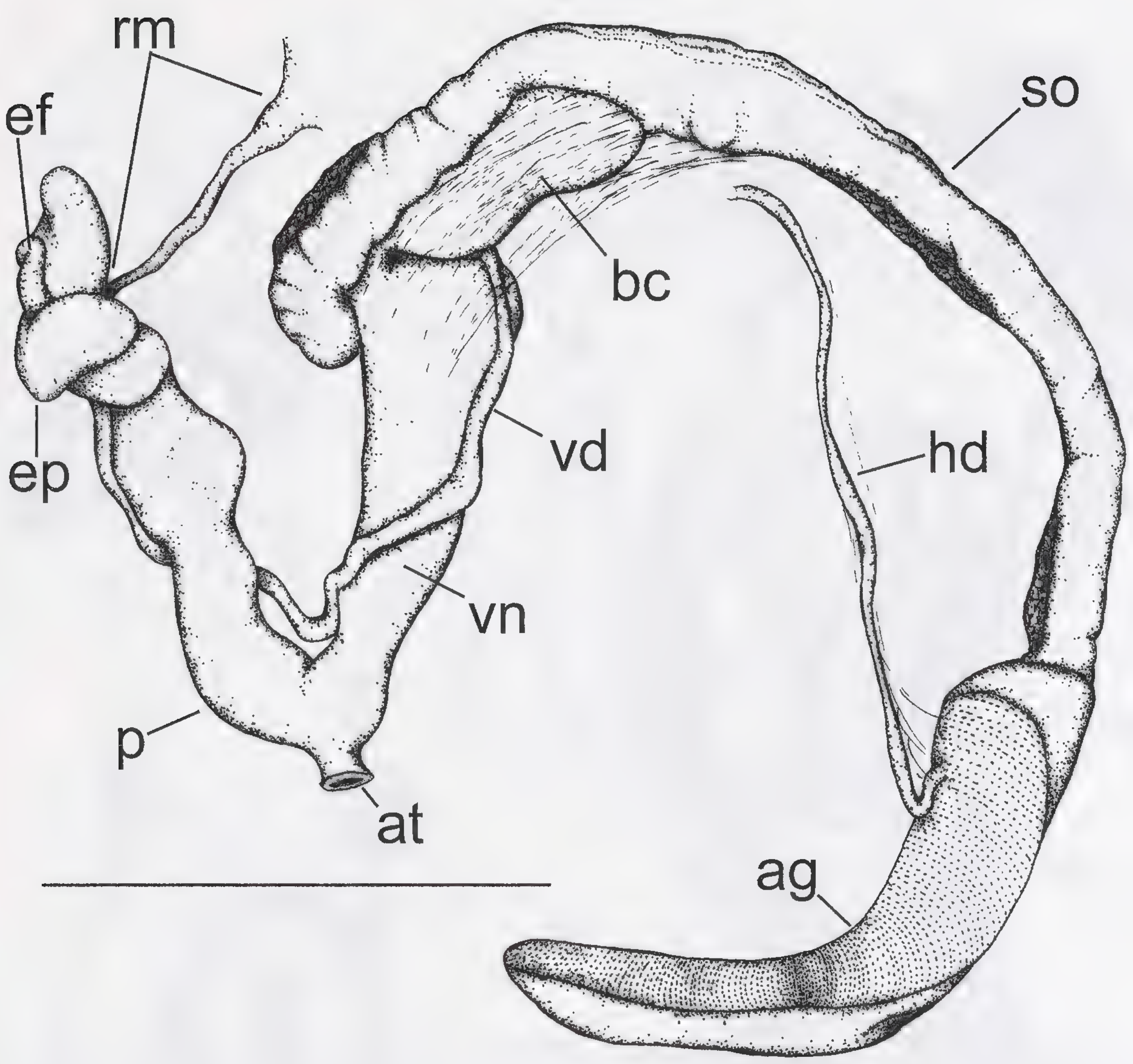

FIG. 87. Genital anatomy of ***Rhagada felicitas*** n. sp. holotype WAM S58487 (Storr Island, May). Scale bar = 3 mm.

last whorl well rounded above and below periphery; umbilicus closed (~ 1/3 of adults) or forming a chink (~ 2/3 of adults); background colour brownish horn to whitish; supra-peripheral band usually strongly developed, moderately thick, distinct, visible on all to most whorls; subsutural band varies from absent to thick, additional spiral bands thinner and lighter in colour, varying in number from one to three above, nil to two below supra-peripheral band, in development from diffuse to distinct; inner lip colour white. Protoconch ~ 2.6 mm in diameter, with 1.5 whorls, smooth. Teleoconch smooth with faint radial growth lines. Angle of aperture ~ 45°; last whorl abruptly descending behind lip; outer lip rounded, slightly expanded, basal node of lip weak, palatal node absent.

Genital anatomy and *head wart* (Figs. 87–88): Penis moderately long, tubular with moderately long, tightly coiled epiphallus, short epiphallic flagellum; penial wall thick proximally, thin distally, interiorly with well-developed longitudinal pilasters comprising entire length of inner wall, pilasters join proximally; strong, corrugated main pilaster at centre of wall; inner epiphallic wall with two weak longitudinal pilasters; penial verge moderate in size, conical, with pointed tip, extending about half of length of penial chamber, with regular lateral corrugations; simple, small groove. Vagina elongated, distally inflated; free part of oviduct very short, coiled; bursa copulatrix tubular, short, strongly inflated, extending anterior end of spermoviduct, not coiled or kinked. Head wart small, broad, irregularly shaped (Fig. 88C).

Mitochondrial Differentiation

Two specimens sequenced; infraspecific genetic distance 0.01; interspecific genetic distance: 0.19–0.22 all other congeners.

Comparative Remarks

Genetic distance to all other sequenced *Rhagada* samples supporting status as distinct species. Most characteristic features are well-developed longitudinal pilasters of inner penial wall, including corrugated main pilaster, laterally corrugated penial verge, and inflated bursa copulatrix, with undifferentiated head. Probably identical with '*Rhagada* species 2' listed by Solem (1991).

Distribution (Fig. 78)

Storr Island, Doubtful Bay, possibly also on adjacent mainland.

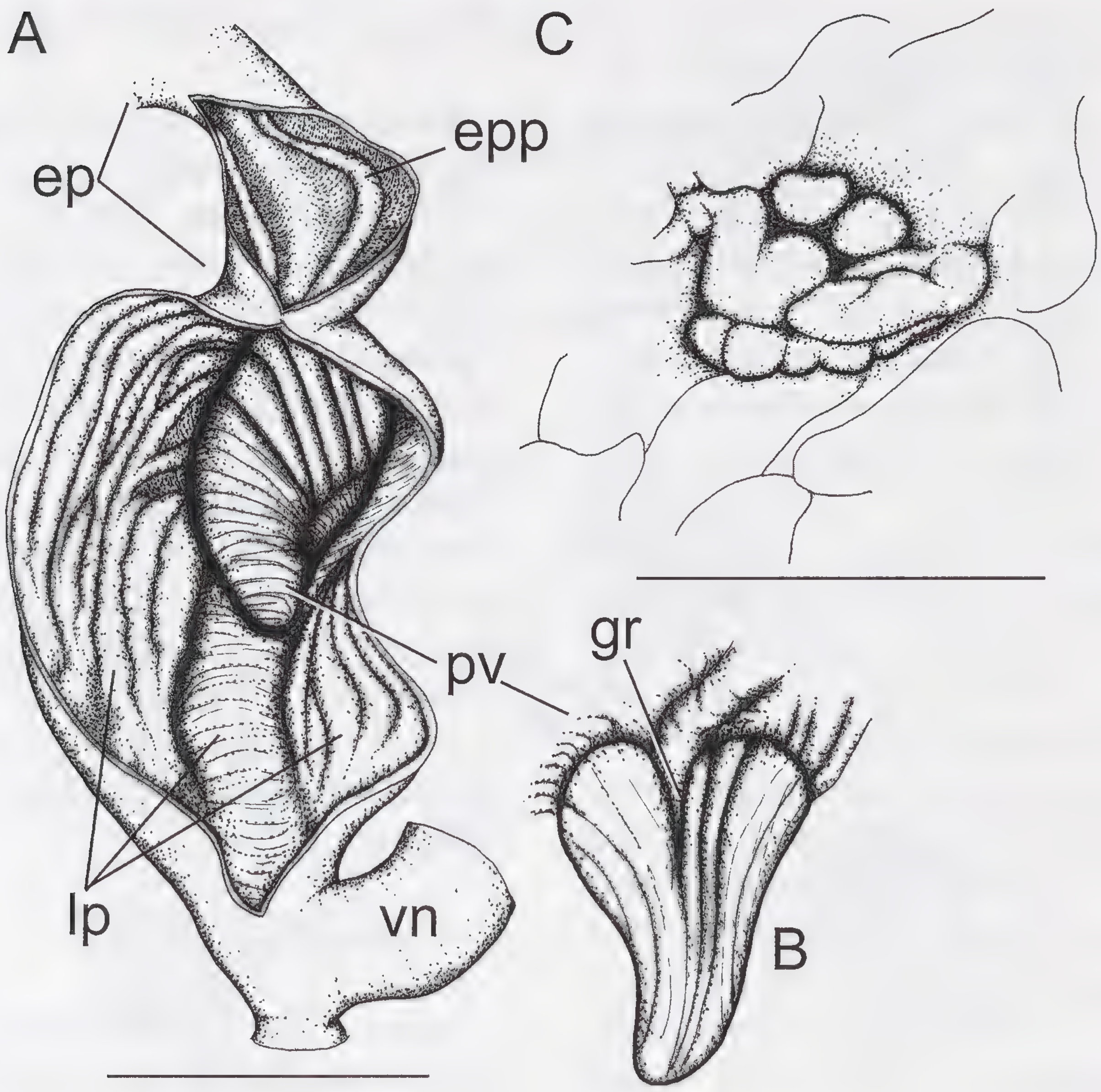

FIG. 88. Penial anatomy and head wart of ***Rhagada felicitas*** n. sp. holotype WAM S58487 (Storr Island, May). A: Penial anatomy; B: Magnification of backside of penial verge; C: Head wart. Scale bars = 1 mm.

Rhagada cygna Solem, 1997
Figs. 79E–F, 89–90

Rhagada cygna Solem, 1997: 1785–1789, pl. 210e–f, 226a–f, figs. 429d–f, 431a, b, 432a–c.

Type Locality

Western Australia, southwestern Kimberley, northern tip of Dampier Peninsula, Cygnet Bay, Pearl Fisheries, One Arm Point, 16°27'13"S, 123°02'40"E.

Material Examined

AM C463537 (preserved specimens) from Gambanan, NW One Arm Point, Dampier Peninsula; AM C463559 (preserved specimens) from Bully's Camp, Cygnet Bay, Dampier Peninsula; AM C463564 (preserved specimens) from Skeleton Point, Dampier Peninsula; WAM S37739 (5 preserved specimens), WAM S49233 (4 preserved specimens), AM C471877 (2 shells), WAM S37831 (7 shells) from Old Mission area, central part of Sunday Island, 16°24'47"S, 123°10'45.5"E; WAM S49231 (8 preserved specimens), AM C471878 (4 preserved specimens) from eastern section of Sunday Island, 16°25'20"S, 123°12'45"E; WAM S49232 (10 preserved specimens), from southern section of Sunday Island, 16°25'55"S, 123°11'28"E; WAM S37728 (preserved specimen, dissected), AM C471879 (10 preserved specimens), WAM S49236 (25 preserved specimens) from Buccaneer Archipelago, northwestern section of Hidden Island, 16°13'29"S, 123°26'51"E and 16°12'50.5"S, 123°27'31.8"E.

Diagnosis

Shell: Small to medium sized (D = 10–14 mm; Table 5), thin but solid, broadly conical with moderately elevated spire with 4.4–5.4 whorls and strongly elevated apex; periphery of last whorl well rounded to slightly depressed (Fig. 79E, F). Protoconch nearly smooth (comprising less than a whorl followed by sharp transition to teleoconch; Fig. 89A, D). Teleoconch with growth pauses and prominent radial ridglets (Fig. 89B, C, E, F). Umbilicus closed in 2/3 of adults, narrowly open in 1/3 of adults; background white, with reddish brown suffusion on spire, supra-peripheral band usually well developed, moderately thick, distinct, visible on all to most whorls; subsutural band varies from thin to absent, additional spiral bands thinner and lighter in colour, usually diffuse, reddish brown colour, varying in number from one to two above, nil to five below supra-peripheral band; inner and outer lip colour white. Last whorl descending slightly behind thin, moderately expanded lip.

Genital anatomy and *head wart*: Penis moderately long, with slightly inflated proper and coiled epiphallus; epiphallic flagellum rather long; penial wall thick proximally, thin distally, interiorly with weak but regular longitudinal folds comprising almost entire length of inner wall, giving rise to well-developed, laterally corrugated pilasters at proximal end; epiphallic wall thick, with indistinct transverse folds or lamellae but no prominent pilasters; penial verge large, extending about half of penial lumen, broadly ovate, smooth, with small, pointed tip; sperm groove stopping well short of tip, long, curved, bounded by thickened margin (Fig. 90A, B). Bursa copulatrix long, kinked. Head wart small, circular (Fig. 90C).

Mitochondrial Differentiation

Sixteen specimens sequenced (eleven from Dampier Peninsula, one from Sunday Island, four from Hidden Island); overall infraspecific genetic distances 0.0–0.05; genetic distances within and between populations from Dampier Peninsula and Sunday Island: 0.012–0.034; on Hidden Island two distinct haplotype groups were found, one being more similar to mainland haplotypes (distances: 0.034–0.045) than to other sequences from the island (0.041–0.047), three other haplotypes from Hidden Island differ from mainland haplotypes by 0.032–0.043 (1 sequence). Interspecific genetic distances: 0.13–0.14 with respect to ***R. dominica*** and ***R. primigena***, and 0.21–0.22 to all other congers.

Comparative Remarks

Genetic distances between local populations are considerable: up to 0.034 between populations on Dampier Peninsula and 0.03–0.05

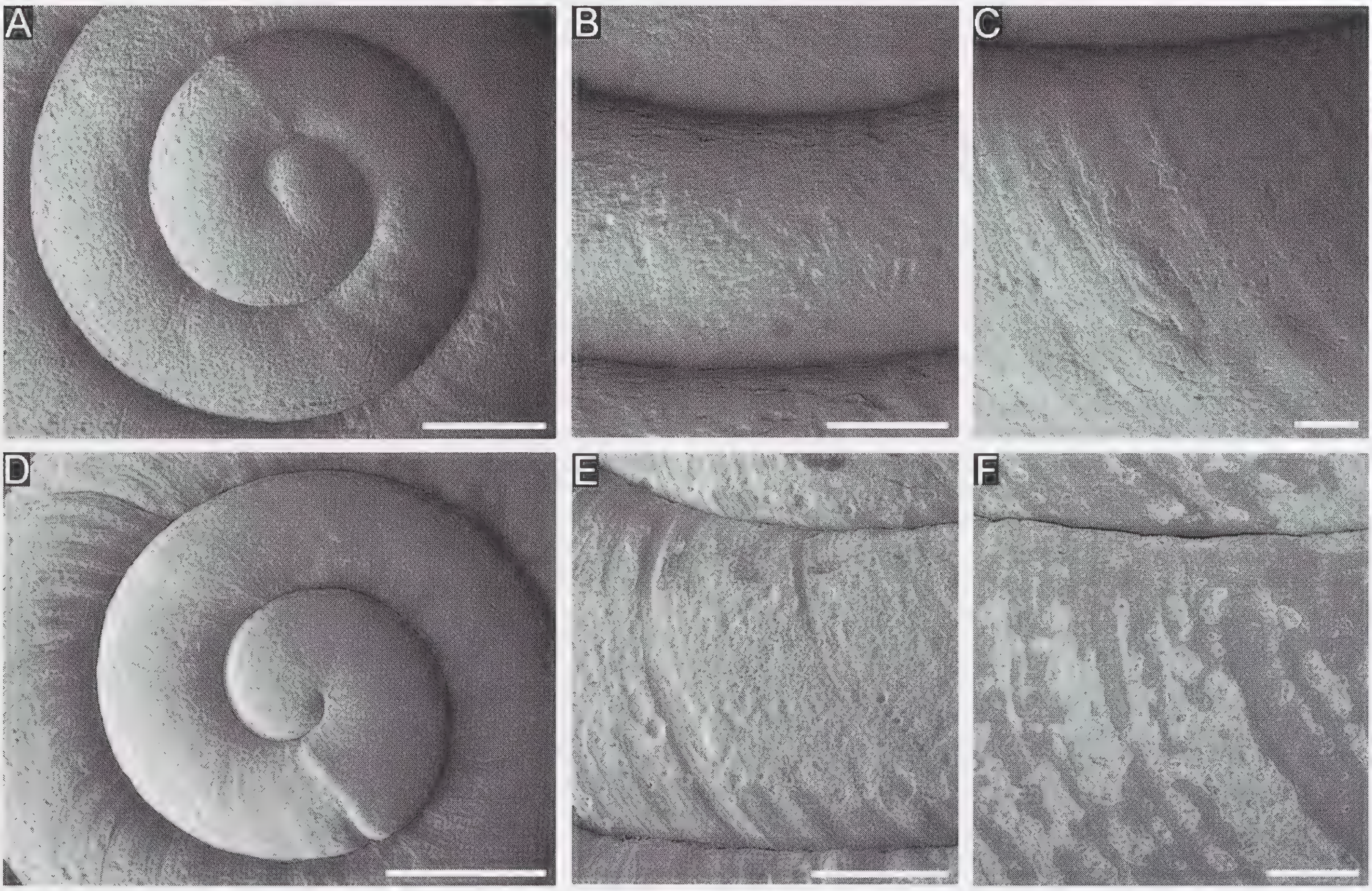

FIG. 89. SEM micrographs of shells of *Rhagada* species. A–C: *Rhagada* cf. *cygna* AM C 471879 (Hidden Island). A: Apical view showing protoconch; B: Close-up of sculpture on second to third whorl; C: Close-up of sculpture on last whorl; D–F: *Rhagada cygna* AM C 471877 (Sunday Island). D: Apical view showing protoconch; E: Close-up of sculpture on second to third whorl; F: Close-up of sculpture on last whorl. Scale bars A, D = 1 mm; B–C, E–F = 500 µm.

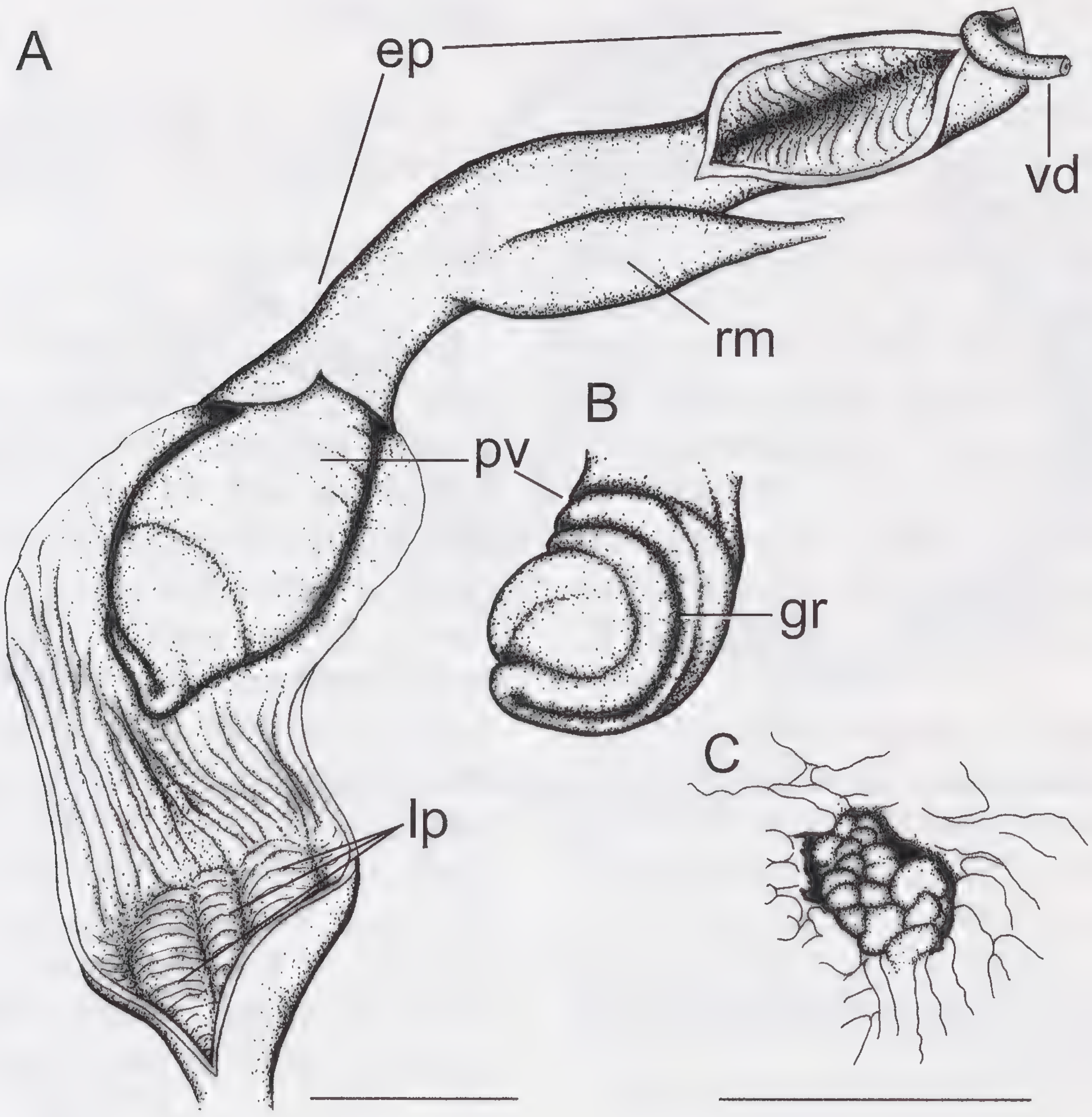

FIG. 90. Penial anatomy and head wart of *Rhagada* cf. *cygna* WAM S37728 (Hidden Island, June). For comparison with anatomy of type material from the Dampier Peninsula compare with Solem (1997: 1788, fig. 432). Scale bars = 1 mm.

between populations from different islands. There is no correlation between genetic and geographic distances. Hidden Island supports two genetically distinct haplotype groups, which indicates more than one past event of over-water dispersal. These haplotypes are nested within the mainland clade. Local genetic differentiation of island and mainland populations is considered to be at the infraspecific level. Morphological differences between local populations are subtle. Anatomy of *R. cygna* from Dampier Peninsula was figured by Solem (1997). Penial anatomy of a specimen from Hidden Island as shown herein in Figure 90 essentially differs by a more rounded tip of verge and more pronounced penial wall sculpture. From other species, *R. cygna* is differentiated by genetic distances of 0.13–0.24. ***Rhagada dominica*** occurring in sympatry on Sunday Island, differs most conspicuously by its larger shell. ***Rhagada primigena*** differs by its on average larger and flatter shell, presence of well-developed epiphallic pilasters and a more elongated penial verge. In most camaenids, including most *Rhagada* species, transition from protoconch to teleoconch shell is not well marked and mostly the protoconch comprises 1.5–2 whorls. The two shells of *R. cygna*, however, reveal a sharp transition between protoconch and teleoconch with the protoconch having only 0.7 whorls.

Distribution (Fig. 78)

Previously known from northern tip of Dampier Peninsula, Cygnet Bay and One Arm Point, only. Here reported from Sunday Island, about 12 km E of One Arm Point, where it is found in sympatry with ***R. dominica*** n. sp., as well as from Hidden Island, King Sound.

Rhagada dominica n. sp.

Figs. 79G, 91A–C, 92, 93

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, King Sound, Old Mission area, central part of Sunday Island, 16°24’47”S, 123°10’45.5”E; coll. Frank Köhler, 06/06/2009, KIS 1–81 (open woodland, grassland, aestivating under rocks).

Material Examined

Holotype WAM S58488 (preserved specimen, Fig. 79G). Paratypes AM C471874 (10 preserved specimens), WAM S37702 (25 preserved specimens), WAM S49235 (15 preserved specimens), AM C471876 (4 shells), WAM S37813 (8 shells) from type locality; WAM S37698 (25 preserved specimens), AM C471875 (7 preserved specimens) from southern section of Sunday Island, 16°25'30"S, 123°10'30"E; WAM S37699 (13 preserved specimens), WAM S37810 (6 shells) from northern tip of Sunday Island, 16°23'28.1"S, 123°10'32.4"E.

Additional, non-type material WAM S37701 (10 preserved specimens), WAM S37811 (7 shells) from southern section, 16°25'37"S, 123°10'35"E; WAM S37701 (10 preserved specimens), WAM S37813 (12 shells) from southern section, 16°25'11"S, 123°10'35"E; WAM S49234 (15 preserved specimens) from 16°25'31"S, 123°10'30"E.

Etymology

In reference to the Italian word for Sunday ("domenica"); noun in apposition.

Description

Shell (Figs. 79G, 91A–C, Table 5): Medium size (large compared to other species), solid, broadly conical with moderately elevated spire; periphery well rounded to slightly angulated; last whorl well rounded above and below periphery; umbilicus closed; background colour rarely white, mostly yellowish to brownish horn; supra-peripheral band varying in development, usually well developed, rather thin to moderately thick, distinct, visible on all to most whorls; subsutural band varies from absent to thick, additional spiral bands thinner and lighter in colour, varying in number from one to three above, nil to seven below supra-peripheral band, in development from diffuse to distinct; inner lip colour white to horn. Protoconch ~ 3.1

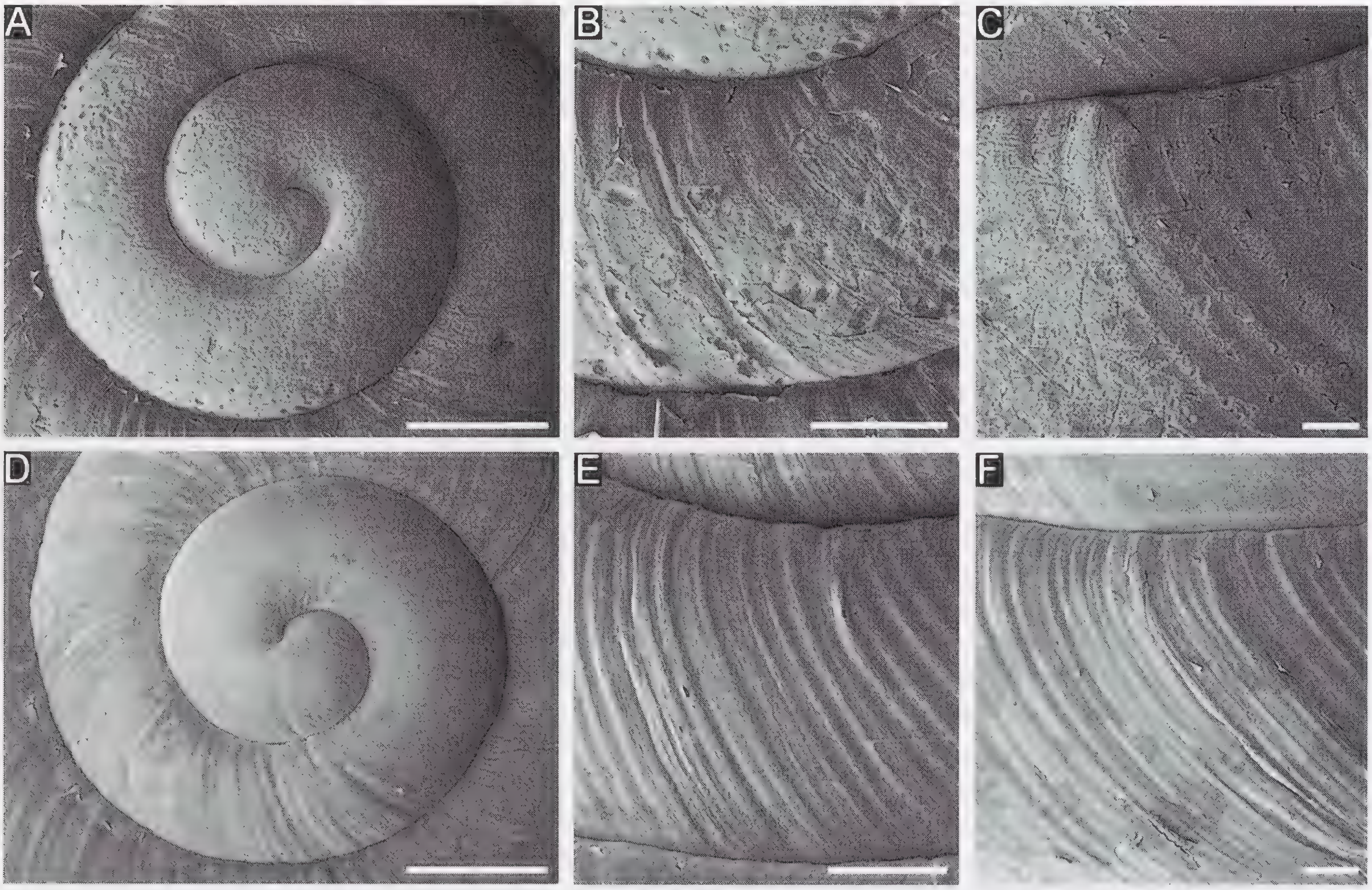

FIG. 91. SEM micrographs of shells of *Rhagada* species. A–C: ***Rhagada dominica*** paratype AM C471876 (Sunday Island). A: Apical view showing protoconch; B: Close-up of sculpture on second to third whorl; C: Close-up of sculpture on last whorl; D–F: ***Rhagada primigena*** paratype AM C471872 (Long Island). D: Apical view showing protoconch; E: Close-up of sculpture on second to third whorl; F: Close-up of sculpture on last whorl. Scale bars A, D = 1 mm; B–C, E–F = 500 μm.

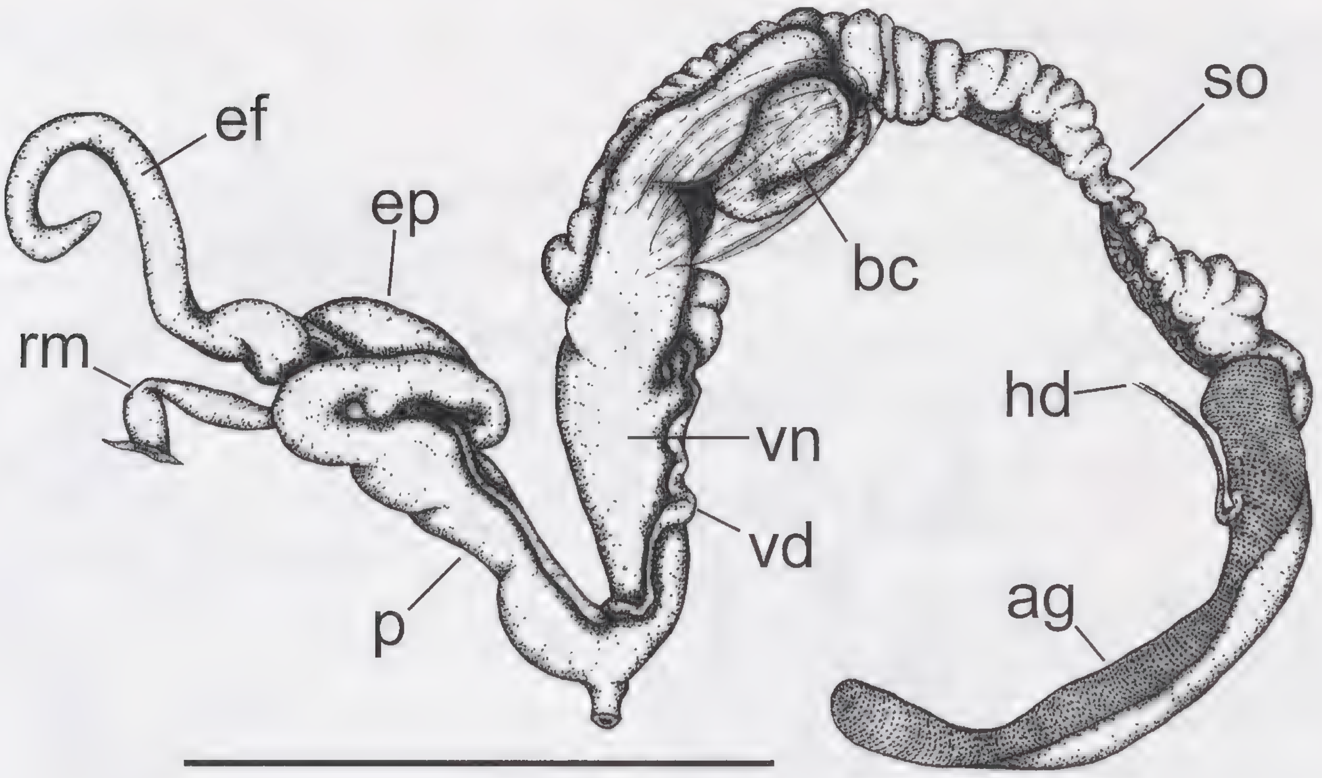

FIG. 92. Genital anatomy of ***Rhagada dominica*** n. sp. paratype AM C471874 (Sunday Island, June). Scale bar = 10 mm.

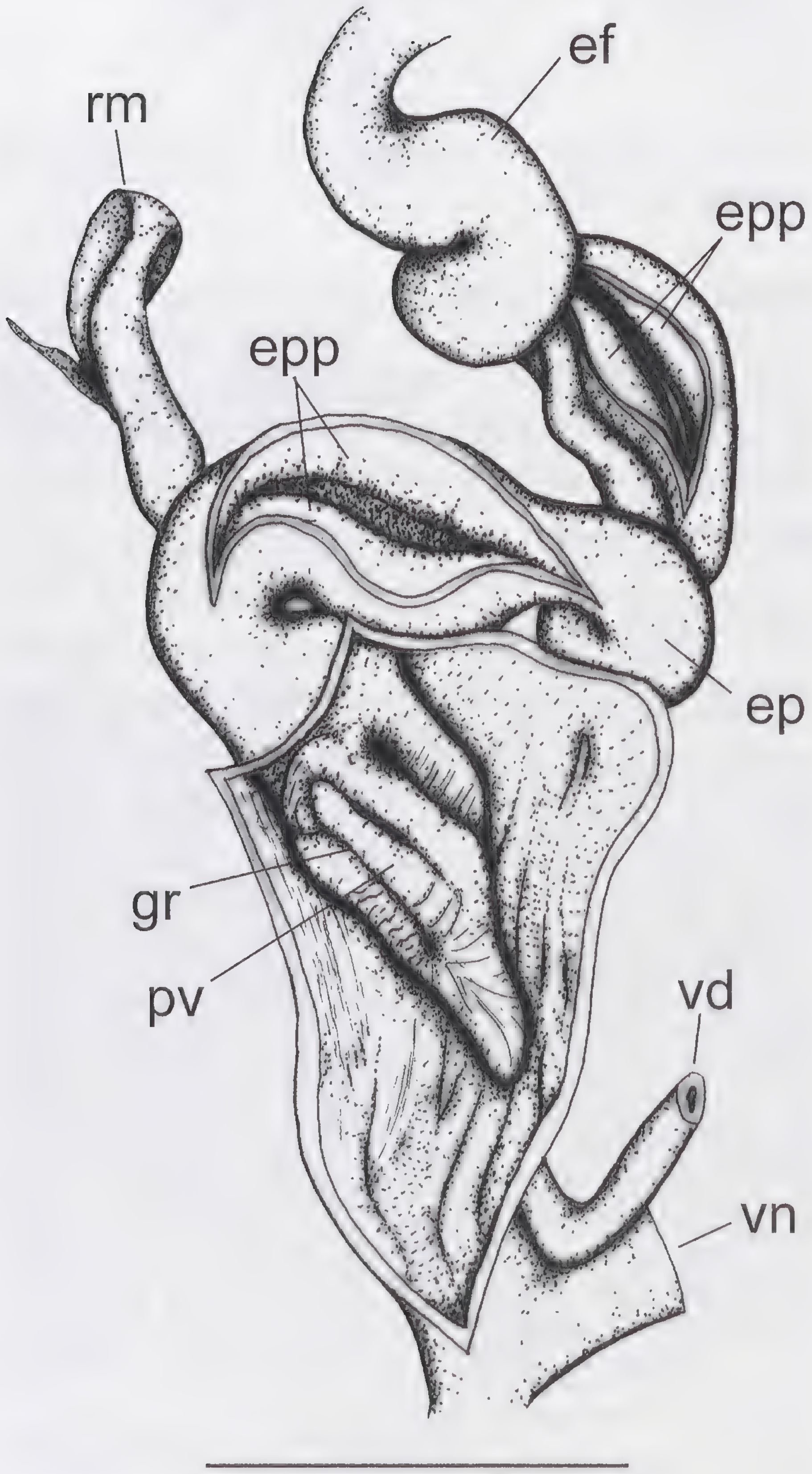

FIG. 93. Penial anatomy and head wart of ***Rhagada dominica*** n. sp. paratype AM C471874 (Sunday Island, June). Scale bar = 3 mm.

mm in diameter, with ~ 1.8 whorls, smooth. Teleoconch smooth with faint radial growth lines. Angle of aperture ~ 45°; last whorl abruptly descending behind lip; outer lip rounded, sharp to thin, slightly expanded, basal node of lip weak, palatal node absent.

Genital anatomy (Figs. 92–93): Penis moderately long, with slightly inflated proper and coiled, long epiphallus; epiphallic flagellum rather long; penial wall thick, interiorly with weak, irregular longitudinal folds comprising proximal part of inner wall; epiphallic wall with two well-developed longitudinal pilasters; penial verge large, conical, pointed extending about half of penial lumen, smooth; sperm groove stopping well short of tip, long, straight. Bursa copulatrix long, kinked.

Mitochondrial Differentiation

Three specimens sequenced; infraspecific genetic distances 0.00–0.02; interspecific genetic distances: 0.03–0.04 with respect to ***R. primigena***, 0.13–0.14 with respect to *R. cygna* and 0.20–0.21 to all other congers.

Comparative Remarks

Genetic distances of more than 13% supporting distinct status with respect to other species except ***R. primigena***, which is not well differentiated by means of genetic distances. However, the latter differs significantly by a smaller size and flatter shape (Table 5). Therefore, it is considered as distinct species despite the low genetic distances.

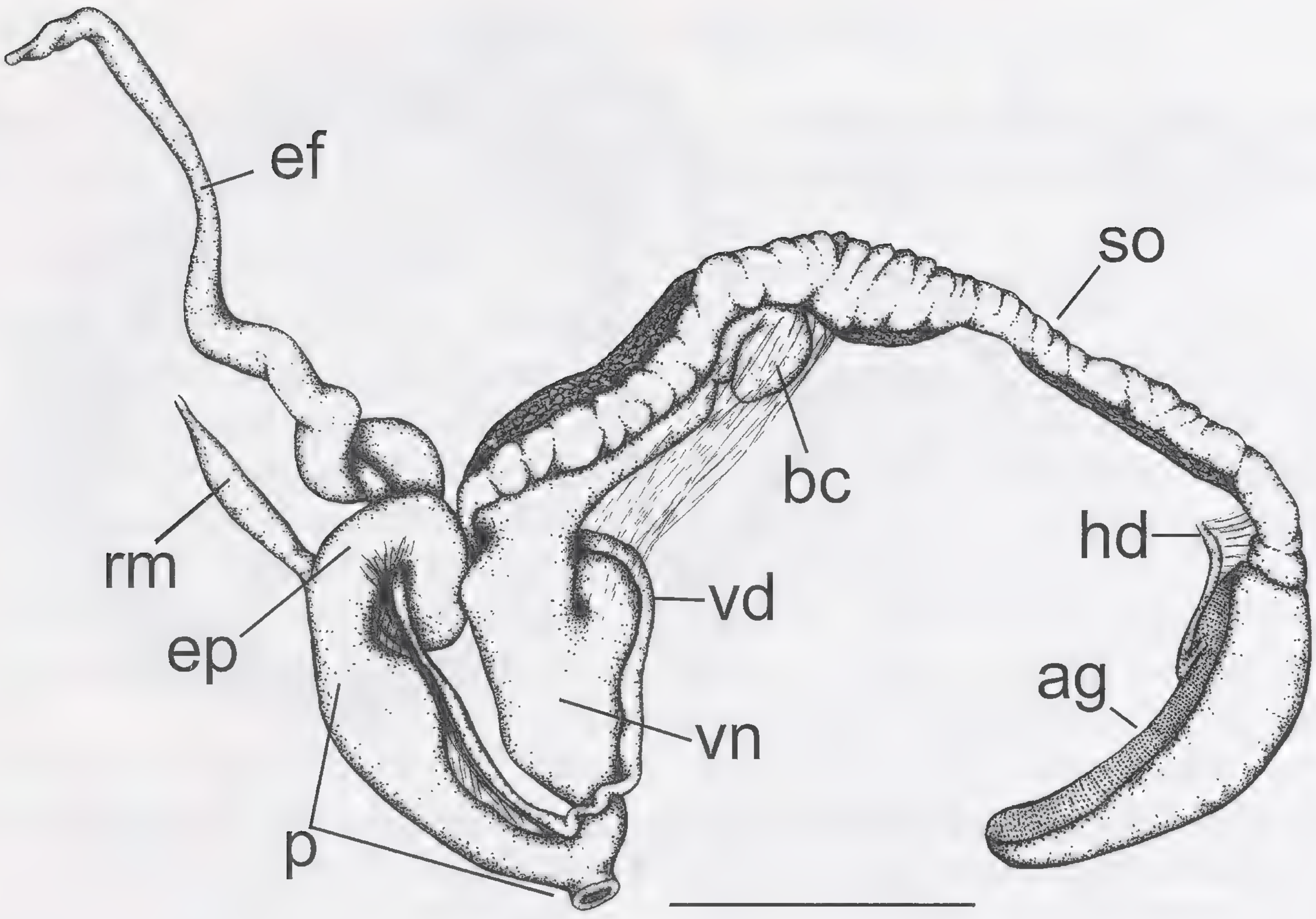

FIG. 94. Genital anatomy of ***Rhagada primigena*** n. sp. paratype AM C471871 (Long Island, May). Scale bar = 3 mm.

Distribution (Fig. 78)

Known from Sunday Island only, where it occurs in sympatry with *R. cygna;* not found on adjacent Dampier Peninsula or other islands.

Rhagada primigena n. sp.
Figs. 79H–I, 92D–F, 94, 95

Type Locality

Western Australia, southwestern Kimberley; Buccaneer Archipelago, King Sound, NE section of Long Island, 16°33'34"S, 123°21'49"E (coll. Frank Köhler, 1/06/2009, KIS 1–76 (gully with dense vegetation, partly overgrown with *Passiflora*; under rocks).

Material Examined

Holotype WAM S37721 (preserved specimen, Fig. 79H). Paratypes AM C471871 (20 preserved specimens), WAM S37719 (31 preserved specimens), WAM S49229 (63 preserved specimens), AM C471872 (6 shells), WAM S37829 (14 shells) from type locality; WAM S37720 (2 preserved specimens), WAM S37721 (preserved specimen), WAM S37830 (3 shells) from 16°33'34–43"S, 123°21'24–49"E.

Additional, non-type material. AM C471873 (4 preserved specimens), WAM S49230 (10 preserved specimens) from largest unnamed island in Fairway Islands Group, West of Long Island, King Sound, 16°34'26.6"S, 123°19'11.2"E.

Etymology

From "*primigenus*" (Latin, masculine = first of all), because this was the first species that I collected myself in the Kimberley; adjective of feminine gender.

Description

Shell (Figs. 79H, I, 91D–F, Table 5): Small to medium sized, thin but solid, broadly conical with low to moderately elevated spire; slightly angulated periphery; last whorl well rounded above and below periphery; umbilicus closed in 80%, narrowly open in 20% of adults; background white to whitish horn, almost completely covered by reddish brown suffusion of spiral bands; supra-peripheral band usually well developed, rather thin to moderately thick, distinct, visible on all to most whorls; subsutural band varies from thin to moderately thick, additional spiral bands thinner and lighter in colour, usually diffuse, blending into each other giving the shell a predominantly reddish brown colour, varying in number from one to three above, nil to many below supra-peripheral band, in development from diffuse to distinct; base of shell with glossy surface, lighter in colour than rest of shell; lip distinctly white. Protoconch ~ 2.4 mm in diameter, with ~ 0.8 whorls, smooth.

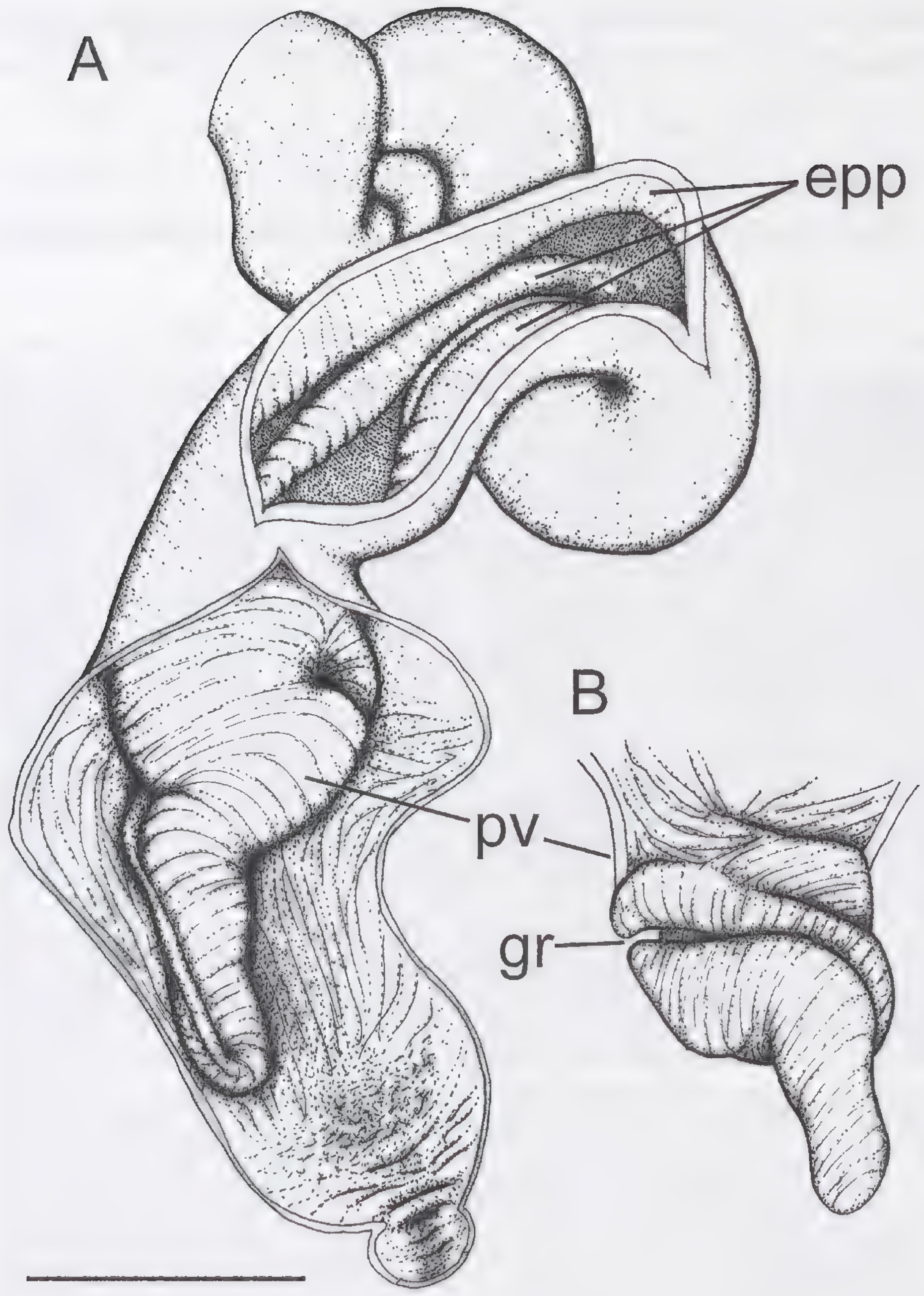

FIG. 95. Penial anatomy of ***Rhagada primigena*** n. sp. paratype AM C471871 (Long Island, May). A: Penial anatomy. Scale bar = 1 mm; B: Magnification of backside of penial verge.

Teleoconch smooth with faint radial growth lines. Angle of aperture ~ 45°; last whorl weakly descending behind lip; outer lip rounded, relatively thick, slightly expanded, basal node of lip weak, palatal node absent.

Genital anatomy (Figs. 94–95): Penis moderately long, with slightly inflated proper and coiled epiphallus; epiphallic flagellum extremely long; penial wall thick proximally, thin distally, interiorly with weak longitudinal folds comprising proximal part of inner wall; epiphallic wall with three well-developed longitudinal pilasters; penial verge large, conical, with elongate-pointed tip, extending more than half of penial lumen, with faint transverse corrugations; sperm groove almost reaching tip, very long, winding, bounded by thickened margins. Vagina short, inflated. Bursa copulatrix long, kinked.

Mitochondrial Differentiation

Five specimens sequenced (three from Long Island, two from Fairway island group); infraspecific distance: 0.00–0.01; interspecific genetic distances: 0.03–0.04 with respect to ***R. dominica***, 0.13–0.14 with respect to *R. cygna* and 0.21–0.24 to all other congers.

Distribution (Fig. 78)

Known from Long Island and Fairway Islands about 6 km W of Long Island, King Sound.

Comparison

Typical combination of features are small size of shell, predominantly reddish brown colouration, glossy base of shell, distinctly white outer and inner lip of shell in contrast with rest of shell. Like *R. cygna*, this species differs from other congeners by smaller protoconch with fewer whorls (< 1 instead of 1.5–2); differs from *R. cygna* by larger shell (Table 5), pointed verge and well-developed epiphallic pilasters.

Retroterra Solem, 1985

Retroterra Solem, 1985a: 787–804; 1991: 209–210; Solem & McKenzie, 1991: 247–263. Type species: *Retroterra costa* Solem, 1985, by original designation.

Diagnosis

Shell: Medium sized to large (D = 13–23 mm; Table 6), thin to moderately thick, discoidal with flat to low spire; umbilicus moderately to widely open (outer diameter > 8 mm), not concealed; protoconch sculpture from rather smooth to consisting of weak to well-developed, radially elongated pustulation; teleococonch with fine to very prominent, narrowly spaced radial ribs, sometimes anastomosing; no significant microsculpture; whorls moderately to rapidly increasing; deep suture; periphery well rounded. Shell colour more or less uniform except for lighter base, yellowish brown to dark brown; no banding.

Genital anatomy: Penis without penial sheath, with well-developed, long and coiled epiphallus supporting epiphallic flagellum of variable length. Penial retractor muscle attached at epiphallus. Epiphallus opens to penial lumen through verge. Vas deferens entering epiphallus laterally at base of flagellum. Bursa copulatrix very long, complexly kinked or coiled.

Aestivation Strategy

Free sealer.

TABLE 6. Shell parameters of *Retroterra* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype; * from Prince Regent Reserve, WAM S49570.

Species	N	Height (H)	Diameter (D)	Umbilical Width	Whorls	H/D Ratio
R. aequabilis n. sp.	HT	13.0	21.8	6.2	4.7	0.60
	6	10.5–13.0 (11.9 ± 1.0)	17.7–23.5 (19.8 ± 2.0)	5.2–8.0 (6.1 ± 0.9)	4.2–5.1 (4.6 ± 0.3)	0.55–0.64 (0.59 ± 0.03)
R. solituda Solem, 1985*	9	10.4–13.0 (11.9 ± 0.9)	20.1–23.6 (22.1 ± 1.2)	5.2–6.5 (5.8 ± 0.4)	4.2–4.9 (4.6 ± 0.2)	0.47–0.57 (0.54 ± 0.03)
R. discoidea n. sp.	HT	6.1	18.6	6.1	3.8	0.33
	14	5.5–7.3 (6.5 ± 0.6)	14.5–18.6 (17.5 ± 1.1)	4.0–6.2 (5.6 ± 0.5)	3.5–4.0 (3.7 ± 0.2)	0.32–0.50 (0.37 ± 0.05)
R. acutocostata n. sp.	HT	6.5	13.6	4.3	3.3	0.48
	5	5.8–7.1 (6.3 ± 0.4)	13.6–17.3 (15.4 ± 1.2)	4.3–5.7 (4.9 ± 0.4)	3.3–3.6 (3.5 ± 0.1)	0.37–0.48 (0.41 ± 0.04)

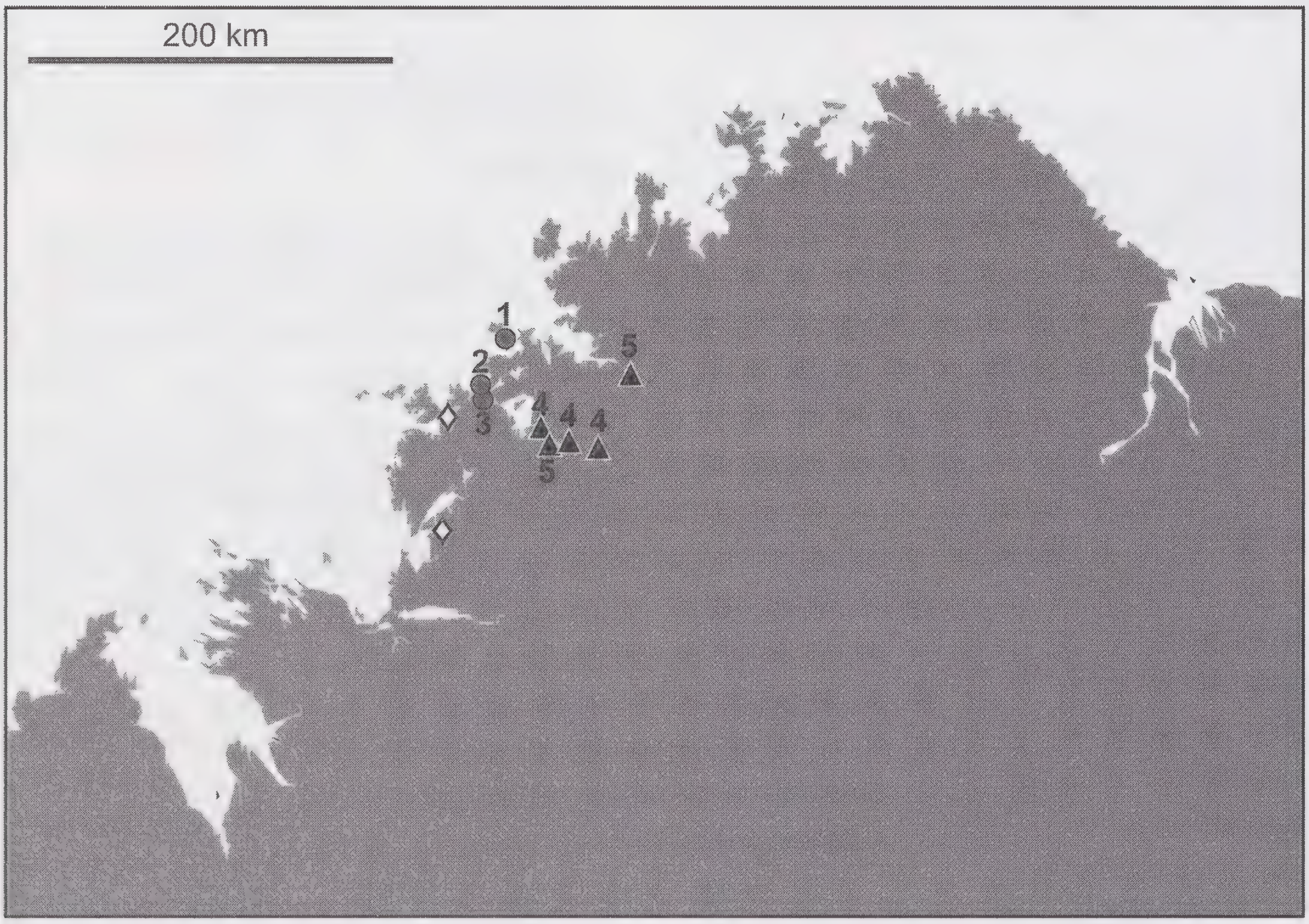

FIG. 96. Distribution map of *Retroterra*. Circles = records of species treated herein: 1: ***R. aequabilis*** n. sp. (Boongaree Island), 2: ***R. discoidea*** n. sp. (Uwins Island), 3: ***R. acutocostata*** n. sp. (Halfway Bay); triangles = records of Solem (1985): 4: *R. solituda* (Prince Regent Reserve), 5: *R. parva* Solem, 1985 (mainland); diamonds = records of undescribed taxa listed by Solem (1991).

Comparative Remarks

The rather large, discoidal shell with wide umbilicus and ribbed sculpture set this taxon apart from all other Kimberley camaenids. *Retroterra* differs from its supposed relative *Baudinella* by larger size, absence of microsculpture, conspicuous ribbing, and weaker expansion of lip. It differs from *Setobaudinia* most conspicuously by ribbing of shell, and

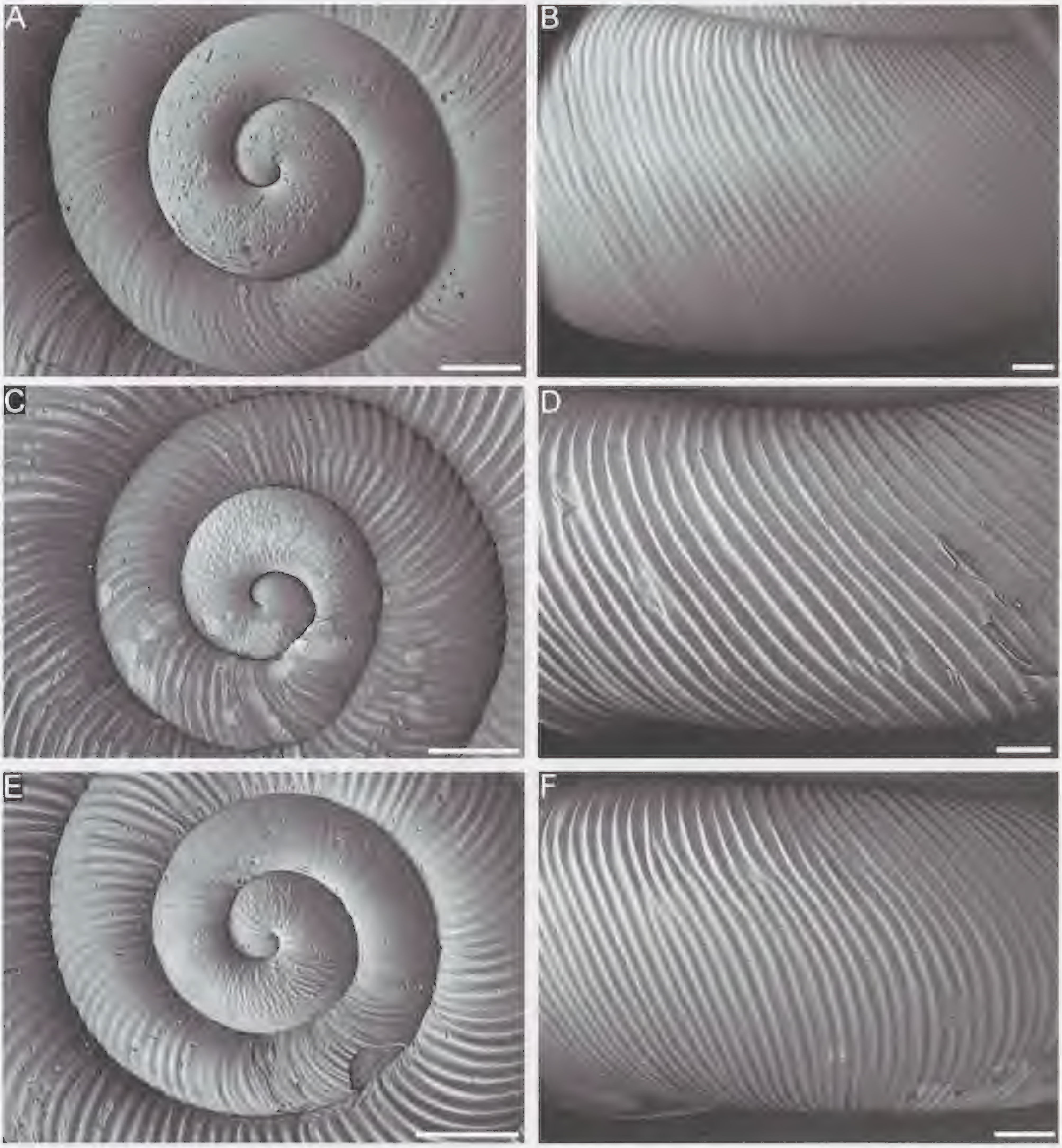

FIG. 97. SEM micrographs of shells of *Retroterra* species. A–B: ***Retroterra aequabilis*** n. sp. paratype WAM S49014 (Boongaree Island). A: Apical view showing protoconch and first whorl; B: Close-up of sculpture on last whorl, lateral view; C–D: ***Retroterra discoidea*** n. sp. paratype WAM S49036 (Uwins Island). C: Apical view showing protoconch and first whorl; D: Close-up of sculpture on last whorl, lateral view; E–F: ***Retroterra acutocostata*** n. sp. paratype AM C471756 (Boongaree Island). E: Apical view showing protoconch and first whorl; F: Close-up of sculpture on last whorl, lateral view. Scale bars = 1 mm.

from *Torresitrachia* by widely open umbilicus; see also Solem (1985a).

Diversity and Distribution (Fig. 96)

Three described and two unnamed species were reported from the Prince Regent Reserve by Solem (1985a, 1991), who pointed out that *Retroterra* seems to be absent from most islands in the Admiralty Gulf and the Mitchell Plateau. Occurrence further south has remained unclear. Here species are reported from Boongaree and Uwins islands, respectively as well as from Hanover Bay area, which fall right within the range circumscribed by Solem (1985a).

Retroterra aequabilis n. sp.

Figs. 79J, 97A, B

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, central section of Boongaree Island, 15°04'30"S, 125°11'21"E; coll. Vince Kessner, 07/02/2009, KIS 1–64 (vine thicket/rainforest on steep upper slopes, in deep leaf litter amongst boulders).

Material Examined

Holotype WAM S58448 (preserved specimen; Fig. 79J), paratypes WAM S37629 (5 preserved specimens), WAM S49015 (shell) from type locality; WAM S36439 (3 shells) from 15°04'36"S, 125°11'12"E; WAM S36440 (shell) from 15°04'15"S, 125°11'14"E; WAM S37628 (preserved juvenile) from 15°03'28"S, 125°10'29"E; WAM S49014 (shell) from 15°03'28"S, 125°10'29"E.

Etymology

From "*aequabilis*" (Latin = similar or equal to), for close similarity with *Retroterra solituda* Solem, 1985, from Prince Regent Reserve; adjective of feminine gender.

Description

Shell (Figs. 79J, 97A, B): Medium to large (D ~ 23 mm on average in fully grown adults; Table 6), with weakly elevated spire and not or weakly descending body whorl. Umbilicus 5–8 mm wide. Protoconch rather smooth (Fig. 97A), extending more than one whorl. Teleoconch with regular, fine, narrowly space radial ribs, not extending onto base of shell and into umbilicus (Fig. 97B). Periphery of last whorl well rounded, separated by rather shallow suture. Shell uniformly dark brown with much lighter, yellowish brown base. Lip of aperture weakly expanded, simple, parietal wall thinly callued.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.089 with respect to *R. solituda* from the type locality of this species (2 sequences), 0.105 to ***R. discoidea*** (1 sequence), and 0.113 to ***R. acutocostata*** (1 sequence).

Comparative Remarks

Genital anatomy remaining unknown for poor preservation or juvenile status of types. Very similar to *R. solituda* Solem, 1985, from Youwanjela Creek, Prince Regent Reserve, Kimberley mainland. Only few worn and poorly preserved specimens are available from Boongaree Island, about 65 km in northwesterly direction from type locality of *R. solituda*, which differs from all other species most conspicuously by larger size and weaker ribs. The decay of examined specimens of ***R. aequabilis*** does not allow for documentation of genital anatomy. Compared with *R. solituda* (topotypes, WAM S49570), ***R. aequabilis*** exhibits subtle differences in shell morphology that per se would not justify recognition as distinct: a generally lighter shell colour, a more indistinct demarcation of the lighter colour field at base of shell, less marked contrast between shell and base colour, a comparatively wider umbilicus (average U/D ratio 3.16 in ***R. aequabilis***, 3.34 in *R. solituda*), smaller average diameter at same shell height (Table 6), and wider cross-section of body whorl, which tends to be more keeled in *R. solituda*. However, molecular phylogenetic data strongly supports treatment as distinct species because in preliminary phylogenetic trees both are shown as two well-differentiated clades, and not in a sister-group relationship (Köhler, unpubl. data).

Distribution (Fig. 96)

Boongaree Island.

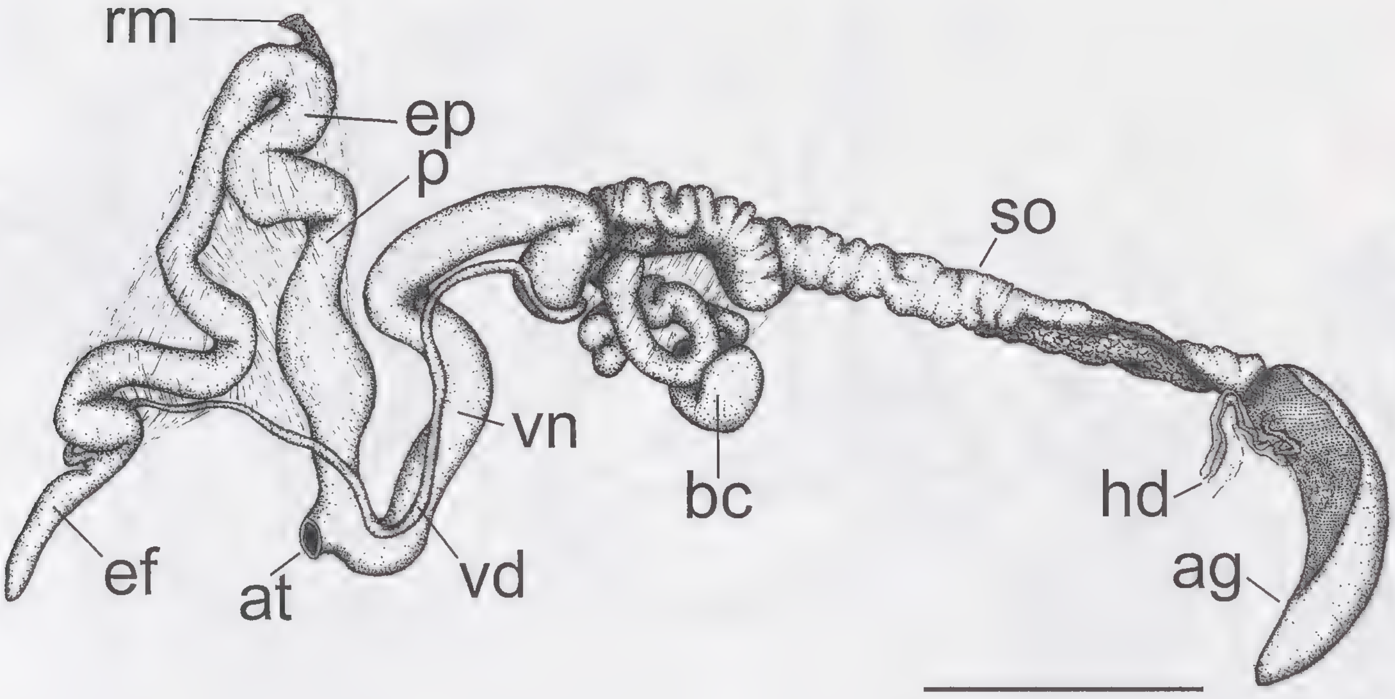

FIG. 98. Genital anatomy of ***Retroterra discoidea*** n. sp. paratype AM C471755 (Uwins Island, June). Scale bar = 5 mm.

Retroterra discoidea n. sp.

Figs. 79K, 97C, D, 98, 99

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Hanover Bay, Uwins Island, 15°15'32"S, 124°48'08"E; coll. Vince Kessner, 9/06/2008, KIS 3–106 (vine thicket, large fig trees on upper slopes, piles of rocks, under large sandstone slabs).

Material Examined

Holotype WAM S58449 (preserved specimen; Fig. 79K, Table 6). Paratypes AM C471755 (10 preserved specimens), WAM S36999 (32 preserved specimens), WAM S37252 (10 shells) from type locality; WAM S37630 (4 preserved specimens), WAM S49036 (shell) from 15°15'32"S, 124°48'08"E.

Additional, non-type material. WAM S37248 (shell) from 15°15'52"S, 124°47'05"E; WAM S37249 (2 shells) from 15°16'02"S, 124°48'09"E; WAM S37250 (5 shells) from 15°15'26"S, 124°48'08"E; WAM S37251 (3 shells) from 15°15'45"S, 124°47'54"E; WAM S48037 (shell) from Myctyis Island, 15°13'12"S, 124°47'23"E.

Etymology

In reference to the discoidal shell; adjective of feminine gender.

Description

Shell (Figs. 79K, 97C, D): Medium sized (D = 17.5 mm on average; Table 6), perfectly discoidal, with very low to slightly sunken spire. Umbilicus 4–6 mm wide. Protoconch with radially extended, well-developed pustulation, about one whorl (Fig. 97C). Teleoconch with strongly developed, regularly spaced axial ribs; ribs rounded in cross-section, running slightly sinuate across shell diameter, extending onto base of shell and into umbilicus (Fig. 97D). Apertural lip weakly to well produced, slightly reflected, parietal wall with well-developed callus, weakly descending, forming a angle of about 60°; nodes absent. Colour uniformly dark brown with only slightly lighter base.

Genital anatomy (Figs. 98–99): Penis moderately long; inner penial wall with complex, irregular pattern of oblique pilasters; their ends being interconnected through two lateral pilasters. Epiphallus very long, coiled; inner epiphallic wall with strongly developed longitudinal fold formed by two parallel running, adjacent longitudinal pilasters comprising entire length, plus more indistinct additional pilaster at anterior end; epiphallus opens to penial lumen through large, conical, pointed verge (Fig. 99A, B). Epiphallic flagellum comparatively long. Vagina tubular, long (much longer than free oviduct). Bursa copulatrix moderate in length, thin, coiled, extending base of spermoviduct, with kinked, slightly inflated head, entirely enclosed in tight connective tissue, connected to base of spermoviduct (Fig. 98).

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.089 with respect to ***R. acutocostata*** (1 sequence), 0.105 to ***R. aequabilis*** (1 sequence), and 0.123 to *R. solituda* (2 sequences).

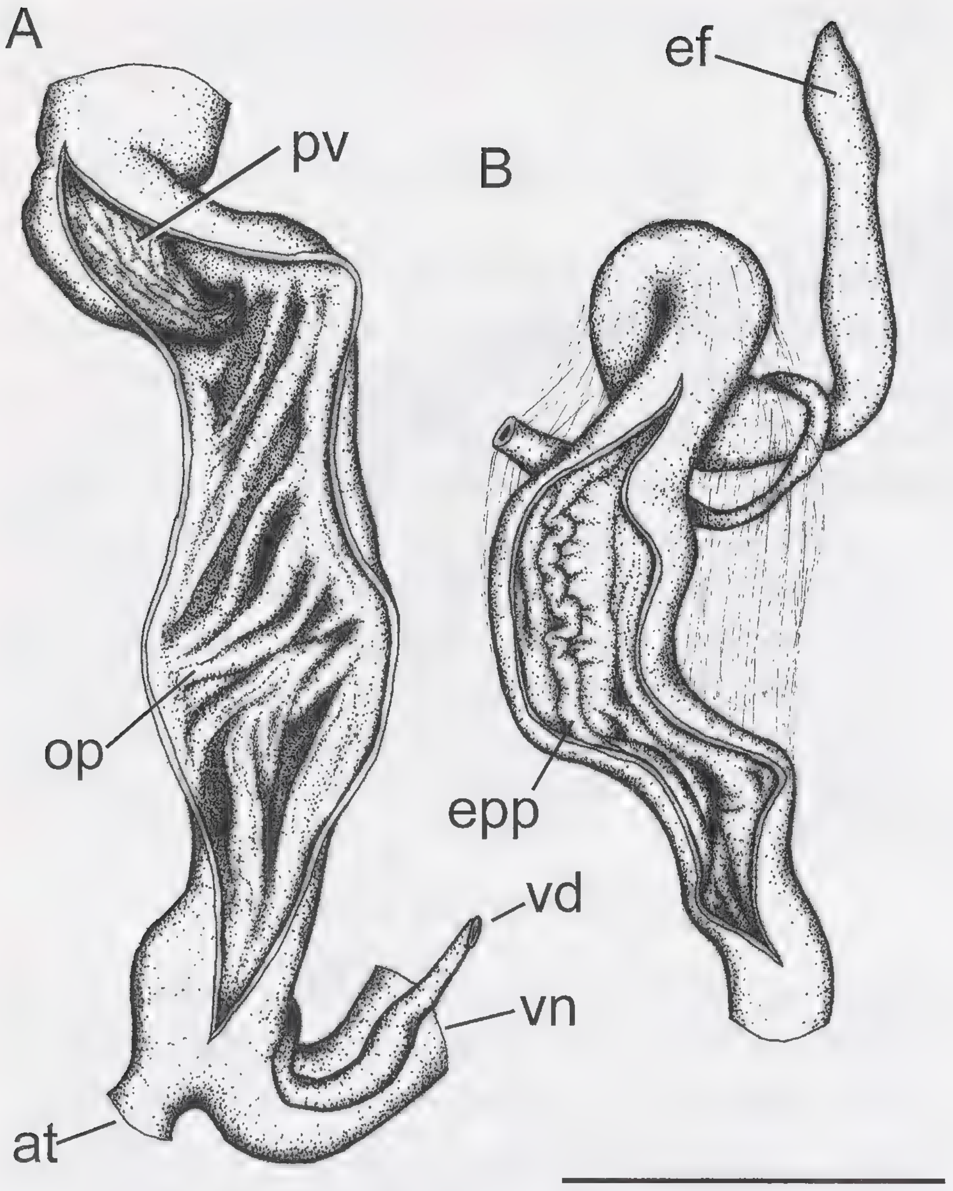

FIG. 99. Penial anatomy of **Retroterra discoidea** n. sp. paratype AM C471755 (Uwins Island, June). A: Section of the penial proper; B: Section of epiphallus. Scale bar = 3 mm.

Comparative Remarks

Most similar to *R. costa* in shell shape, size and sculpture (Table 6); the former being slightly smaller (D = 13.4–19.4 mm), with slightly more elevated spire, larger shell height (5.3–9.2 mm) and H/D ratio (0.43 on average). *Retroterra costa* differs by more regularly coiled bursa copulatrix, being kinked in ***R. discoidea***. *Retroterra solituda* has a larger shell with more elevated spire and differs most conspicuously in armature of inner penial and epiphallic walls.

Distribution (Fig. 96)

Uwins and Myctyis islands.

Retroterra acutocostata n. sp.

Figs. 79L, 97E–F, 100, 101

Type Locality

Western Australia, central Kimberley coast, Hanover Bay, Munster Water, 1.3 km S of Halfway Bay, 15°20'15"S, 124°49'23"E; coll. Vince Kessner, 11/02/2009, KIS 3–133 (S-facing vine thicket at the base of sandstone cliffs; in leaf litter).

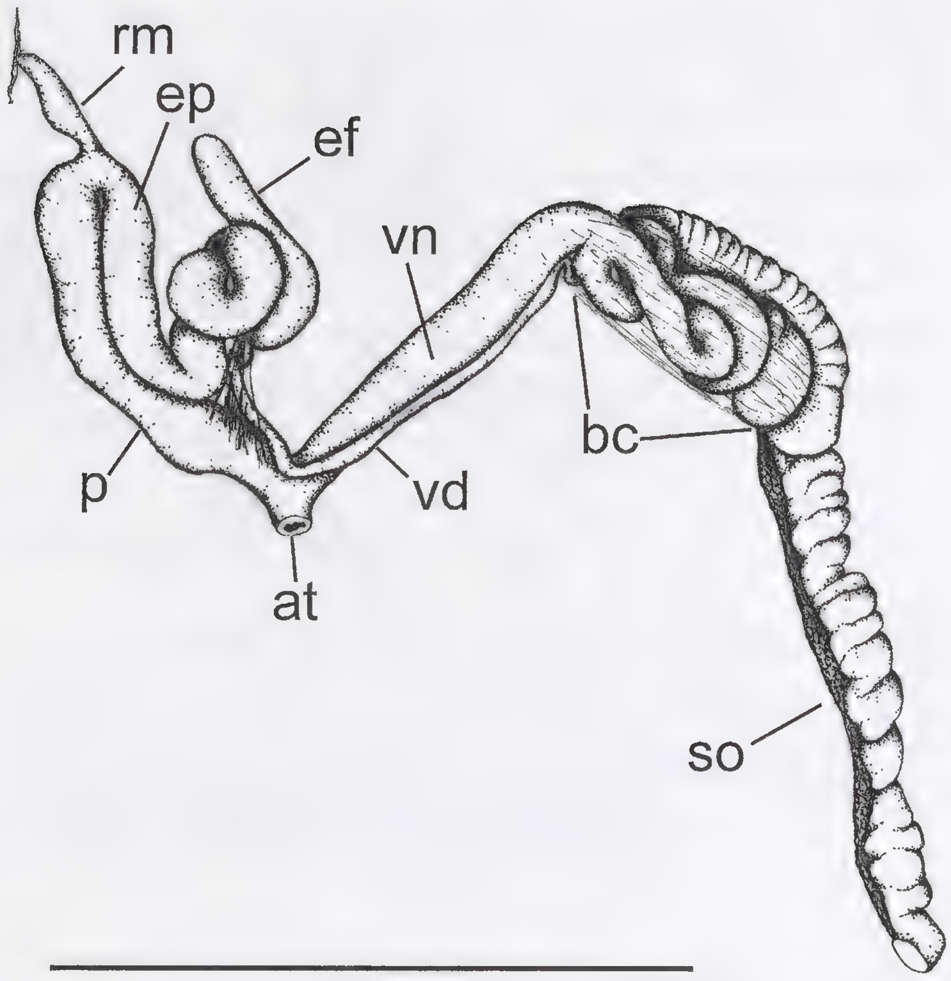

FIG. 100. Genital anatomy of ***Retroterra acutocostata*** n. sp. holotype WAM S58450 (albumen gland lacking). Scale bar = 10 mm.

Material Examined

Holotype WAM S58450 (preserved specimen; Table 6). Paratypes WAM S37644 (3 preserved specimens), WAM S49033 (3 shells), from type locality.

Etymology

In reference to the strong and acute ribs, derived from "*acutus*" (Latin = sharp) and "*costatus*" (Latin = ribbed); adjective of feminine gender.

Description

Shell (Figs. 79L, 97E, F): Medium sized (D = 15.4 on average; Table 6), nearly discoidal, with low spire. Umbilicus 4 mm wide. Protoconch with weak, radially extended pustulation, extending more than one whorl (Fig. 97E). Teleoconch with strongly developed, regularly spaced spiral ribs; ribs pointed in cross-section, running slightly sinuate across shell diameter, extending onto base of shell and into umbilicus (Fig. 97F). Apertural lip weakly produced, slightly reflected, parietal wall thinly callued; nodes absent. Colour uniformly dark brown including base of shell.

Genital anatomy (Figs. 100–101): Penis moderately long; inner penial wall with strong, corrugated longitudinal pilasters. Epiphallus very

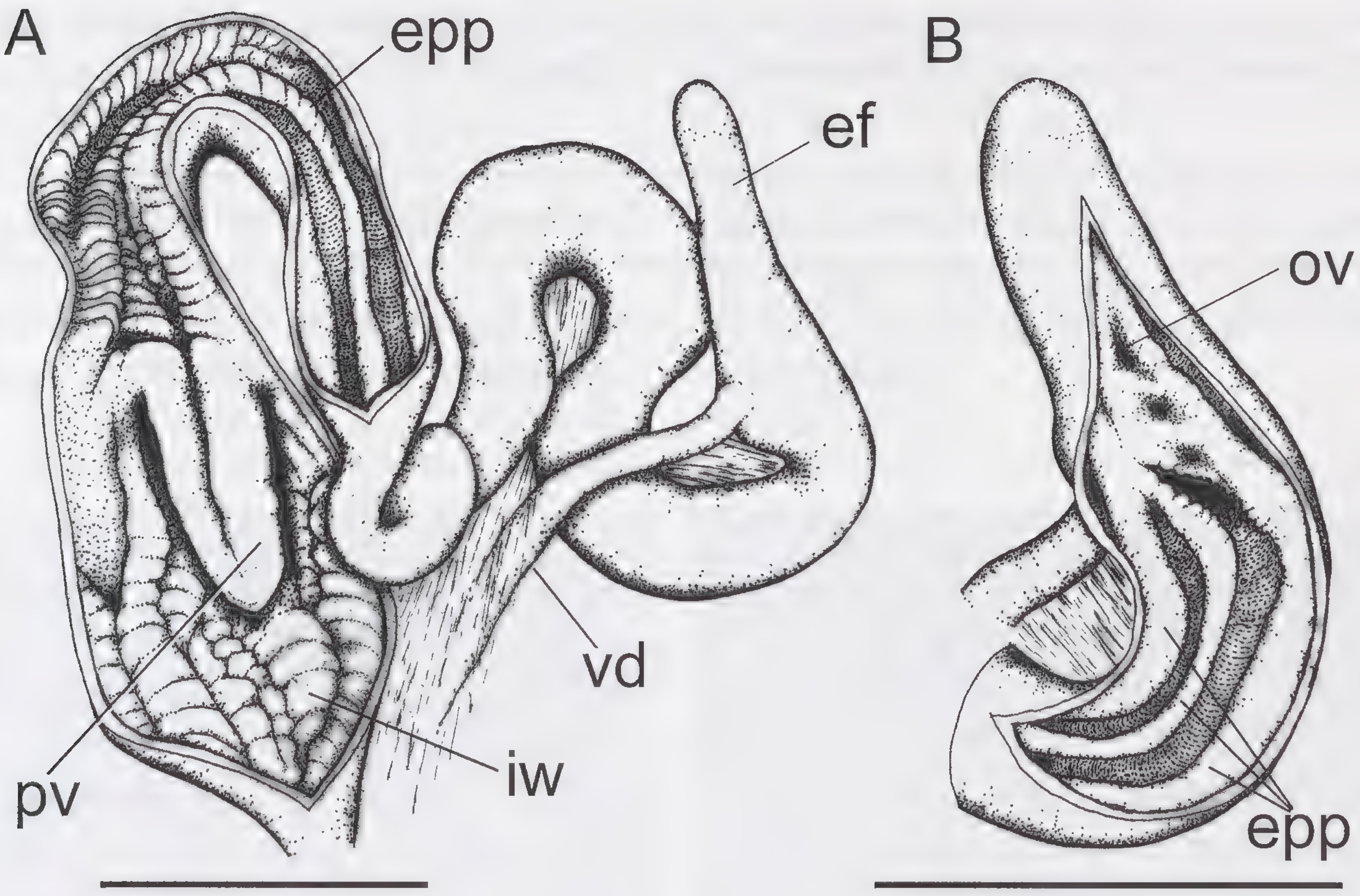

FIG. 101. Penial anatomy of ***Retroterra acutocostata*** n. sp. holotype WAM S58450. A: Section of penis; B: Section of epiphallus. Scale bars = 2 mm.

long, coiled; inner epiphallic wall supporting three longitudinal pilasters comprising entire length, pilasters smooth posteriorly, becoming corrugated anteriorly; epiphallus opens to penial lumen through very large, conical verge. Epiphallic flagellum well developed.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.089 with respect to ***R. discoidea*** (1 sequence), 0.113 to ***R. aequabilis*** (1 sequence), and 0.105 to *R. solituda* (2 sequences).

Comparative Remarks

Shell smaller than in former two species (Table 6); also differing in stronger development of ribs being much weaker in *R. solituda* and not as acute in ***R. discoidea***. Diagnostic feature are conspicuously in thick, corrugated pilasters of inner penial wall.

Distribution (Fig. 96)

Mainland near Halfway Bay, Hanover Bay.

Molema n. gen.

Type Species

Molema stankowskii n. sp.

Etymology

Derived from the name of Molema Island, where the type species occurs; noun of feminine gender.

Description

Shell: Small (D < 10 mm; Table 7), discoidal with flat spire; widely open umbilicus; protoconch with radially arranged, crowded pustules; teleococonch with strong radial ribs, most prominent on last whorl; no well-developed microsculpture; whorls moderately increasing, deep suture; well-rounded periphery.

Genital anatomy: Penis without penial sheath and well-developed epiphallus with short flagellum. Penial retractor muscle attached at distal end of epiphallus. Epiphallus opens to penial lumen through complexly folded vergic ring. Vas deferens entering epiphallus terminally. Bursa copulatrix elongated, kinked, extending anterior end of spermoviduct.

Aestivation Strategy

Free sealer.

Comparative Remarks

Shell similar to *Baudinella* and *Setobaudinia* in overall shape and size, differing by larger

TABLE 7. Shell parameters of **Molema** (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Whorls	H/D Ratio
M. stankowskii n. sp.	HT	3.2	8.9	3.2	0.36
	5	2.8–3.4 (3.2 ± 0.2)	7.8–8.9 (8.4 ± 0.4)	3.0–3.5 (3.2 ± 0.2)	0.36–0.40 (0.38 ± 0.02)

diameter, perfectly dicoidal shape and flat spire, absence of microsculpture or setae, presence of strong, noduled ribs, and absence of apertural nodes. Genitalia similar to *Baudinella* and *Retroterra*, differing most conspicuously by very complex vergic ring that separates lumen of epiphallus and penis as well as by large stimulatory pilaster at posterior end of inner penial wall. In addition, differing from *Retroterra* by shorter and simpler bursa copulatrix and simpler armature of inner penial wall.

Diversity and Distribution (Fig. 102)

One species on Molema Island, Talbot Bay.

Molema stankowskii n. sp.
Figs. 79M, 103–105

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, Talbot Bay, N section of

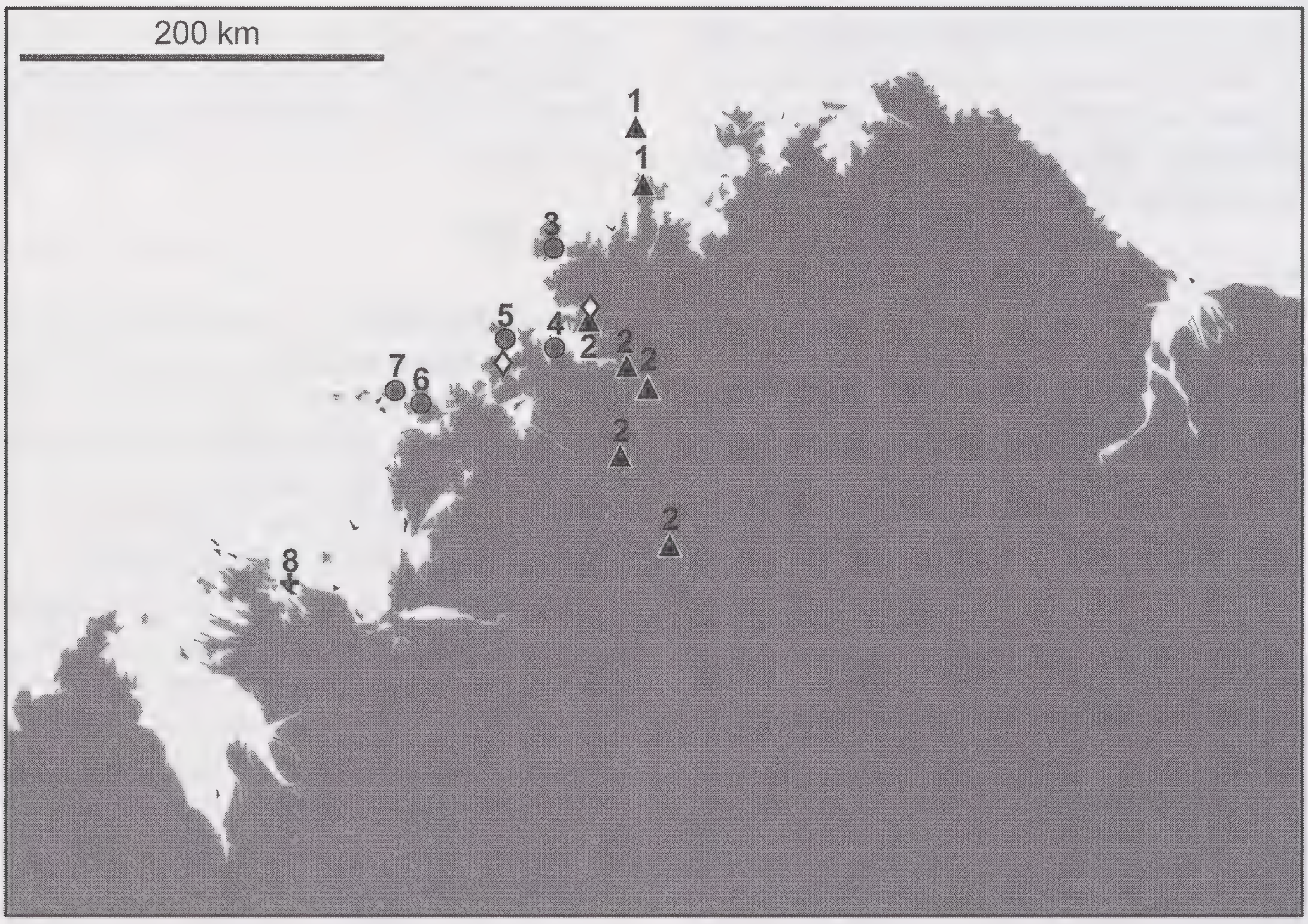

FIG. 102. Distribution map of **Molema** n. gen. and *Baudinella*. Triangles = records of Solem (1985, 1991): 1: *Baudinella baudinensis* (Baudin Island, Bougainville Peninsula), 2: *B. regia* (mainland); circles = new records: 3: ***B. thielei*** n. sp. (Bigge Island), 4: ***B. boongareensis*** n. sp. (Boongaree Island), 5: ***B. tuberculata*** n. sp. (Coronation Island), 6: ***B. setobaudinioides*** n. sp. (Augustus Island), 7: ***B. occidentalis*** n. sp. (D'Arcy Island), 8: ***Molema stankowskii*** n. sp. (Molema Island); diamonds = records of undescribed taxa listed by Solem (1991).

Molema Island, 16°15'02.4"S, 123°49'23.5"E; coll. Sean Stankowski, 30/05/2009, KIS 2–81 (between rocks in soil and litter at base of eucalypts).

Material Examined

Holotype WAM S58447 (preserved specimen; Fig. 79M). Paratypes WAM S37775 (3 preserved specimens), from type locality; WAM S37774 (preserved specimen), from 16°15'09.7"S, 123°49'11.7"E; AM C471753 (preserved specimen), WAM S37773 (3 preserved specimens), AM C471754 (shell), WAM S37899 (2 shells), from 16°15'14"S, 123°29'28"E; WAM S37900 (shell), WAM S37901 (shell), from 16°15'00"S, 123°49'29"E.

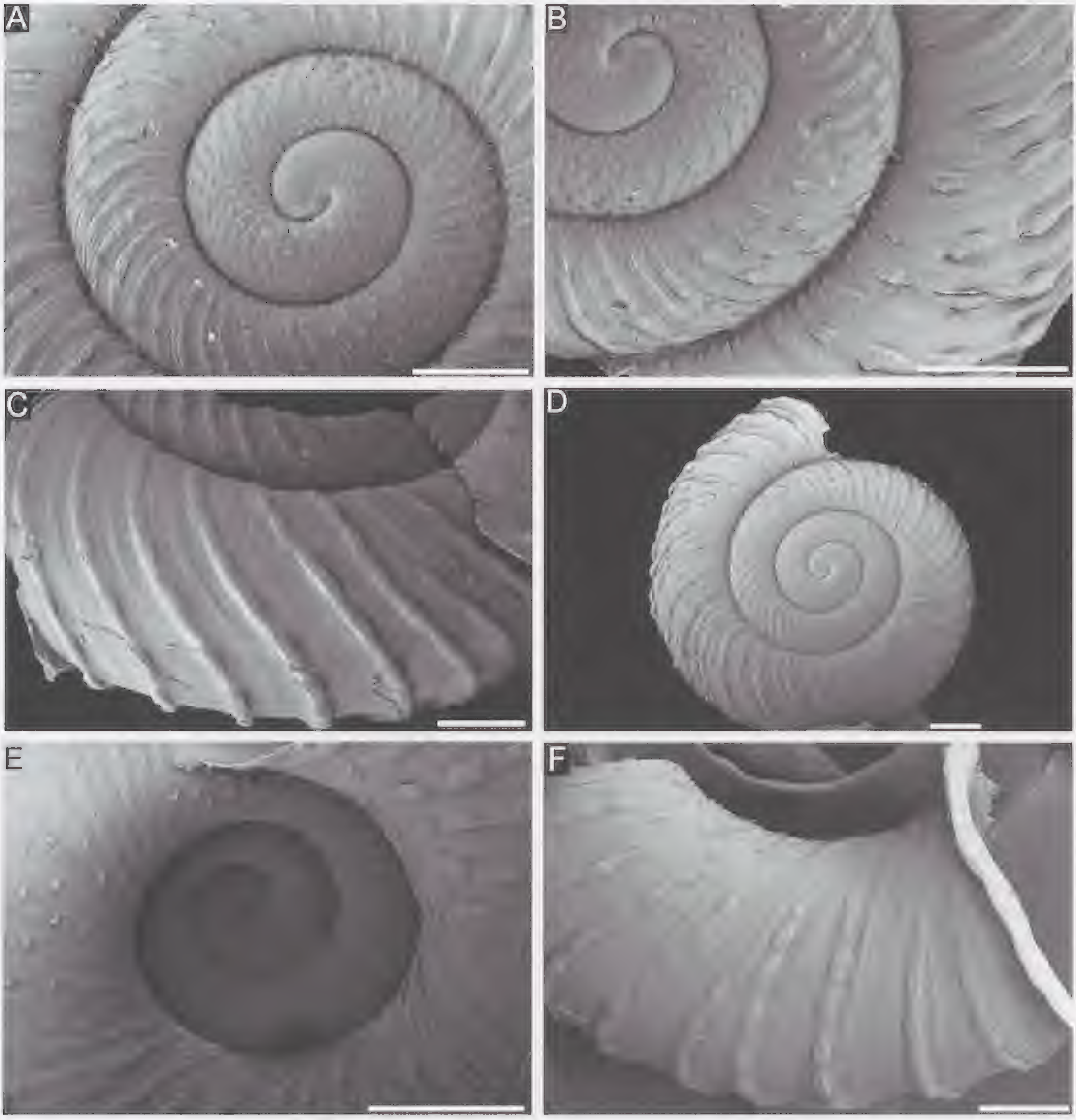

FIG. 103. SEM micrographs of the shell of ***Molema stankowskii*** n. sp. (Molema Island). A–B, D. E: Paratype AM C471754. C, F: Paratype AM C471753. A: Apical view showing protoconch and first whorl; B: Close-up of sculpture across entire shell, viewed from above; C: Close-up of sculpture on last whorl, viewed obliquely from above; D: Entire shell viewed from above; E: Umbilicus viewed from below; F: Sculpture at base of shell and basal lip, viewed from below. Scale bars = 1 mm.

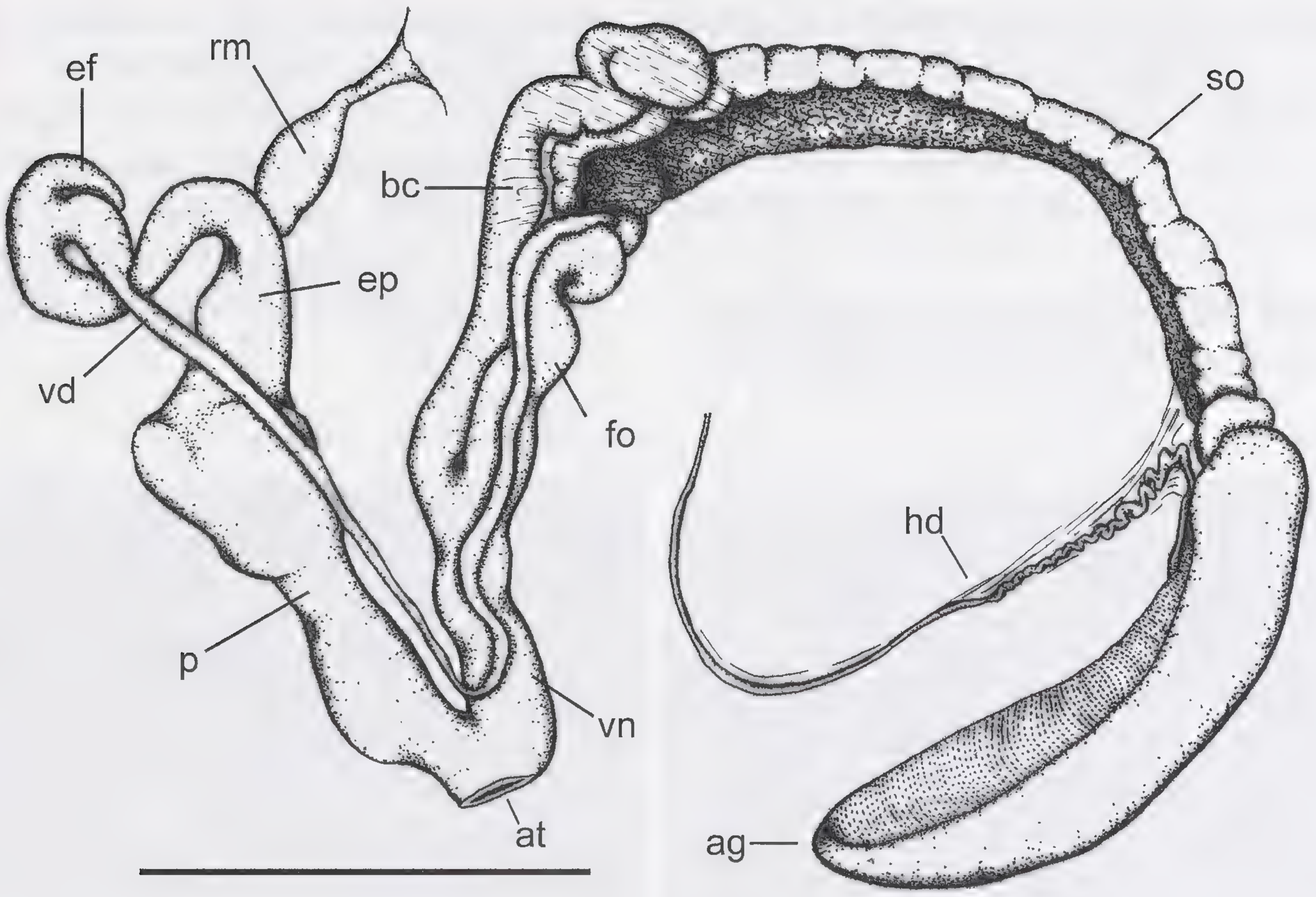

FIG. 104. Genital anatomy of ***Molema stankowskii*** n. sp. paratype WAM S37775 (Molema Island). Scale bar = 3 mm.

Etymology

Named in honour of Sean Stankowski (Perth), who collected the type material, noun in genitive case.

Description

Shell (Figs. 79M, 103): Small (D= 8.4 mm on average, Table 7), perfectly discoidal; body whorl almost not descending. Umbilicus 2.5–3.2 mm wide. Protoconch extending one whorl. Teleoconch with strongly developed, widely spaced radial ribs, most prominent on last whorl; ribs support spiral rows of rounded nodules; which diffuse into radial rows of nodules on base of shell and inner umbilical whorls. Periphery of last whorl well rounded, deeply incised suture. Shell colour uniformly brown. Lip of aperture relatively thin, moderately expanded, weakly reflected, basal edge slightly curved; no prominent palatal or basal nodes; parietal wall very thin.

Genital anatomy (Figs. 104–105): Penis about as long as anterior part of oviduct, with inflated proper; epiphallus about same length as penis, with short epiphallic flagellum near posterior end. Vergic papilla covered by large stimulatory pilaster at proximal end of inner penial wall, which supports fine, dense pustulation on exterior and more strongly developed pustulation on interior surface. Penial wall extremely delicate posteriorly; interiorly supporting several (about six to seven) well developed longitudinal pilasters. Bursa copulatrix elongate, extending anterior end of spermoviduct, head slightly inflated, S-folded, connected to base of spermoviduct by connective tissue.

Distribution

Molema Island, Talbot Bay.

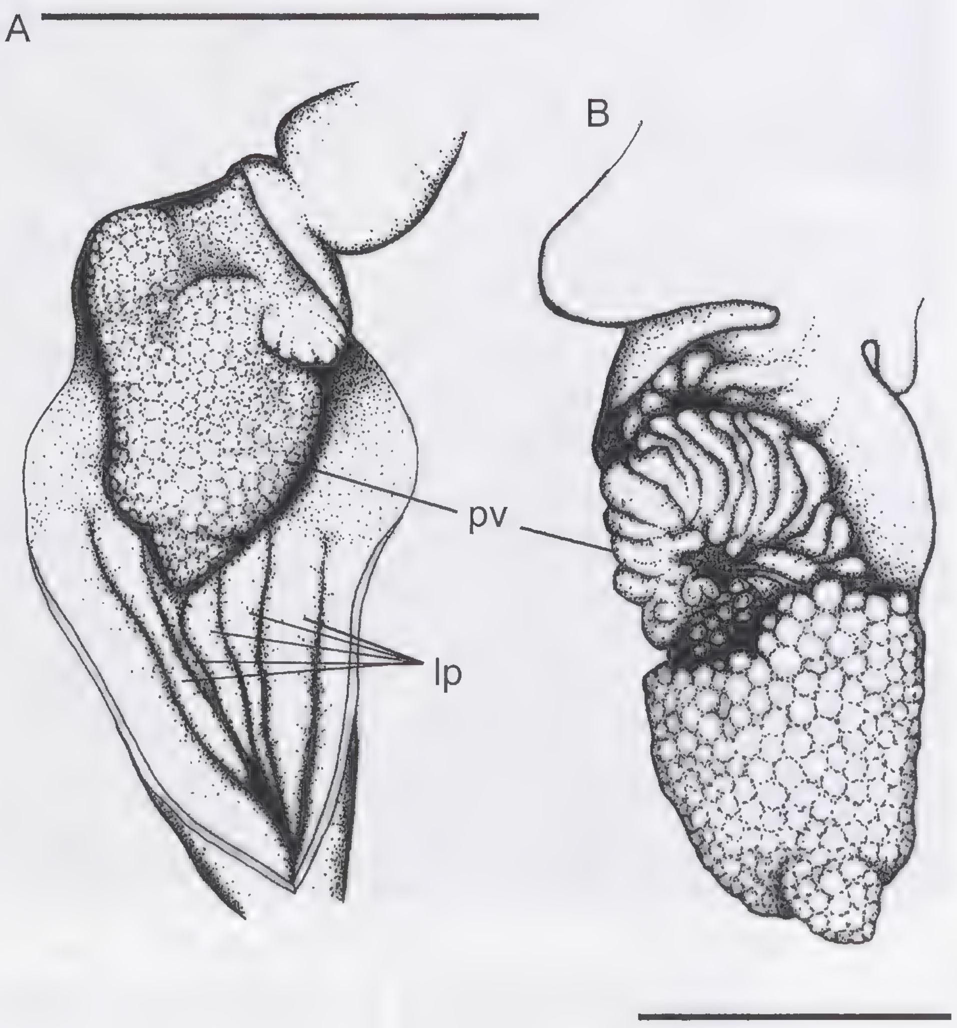

FIG. 105. Penial anatomy of ***Molema stankowskii*** n. sp. paratype WAM S37775 (Molema Island). A: Penial anatomy. Scale bar = 2 mm; B: Backside of penial verge in detail. Scale bar = 1 mm.

Baudinella Thiele, 1931

Baudinella Thiele, 1931: 685. Iredale, 1938: 109; 1939: 49; Solem, 1985a: 775–787; 1991: 207–209; Solem & McKenzie, 1991: 247–263. Type species: *Helix* (*Gonostoma*) *baudinensis* E. A. Smith, 1893, by original designation.

Gonobaudinia Iredale, 1933: 55. Type species: *Helix* (*Gonostoma*) *baudinensis* E. A. Smith, 1893, by original designation.

Taxonomic Remarks

The two generic names *Baudinella* Thiele, 1931, and *Gonobaudinia* Iredale, 1933, were introduced for the same type species, *Helix* (*Gonostoma*) *baudinensis* E. A. Smith, 1893, and are therefore objective synonyms; the older name *Baudinella* having priority. Solem (1985a) described the anatomy and provided a comprehensive overview of its taxonomic history. He also described a second species, *Baudinella regia* Solem, 1985, from Prince Regent Reserve.

Diagnosis

Shell: Small (D = 6.5–7.5 mm; Table 8), discoidal with flat to moderately elevated spire; umbilicus moderately to widely open, not concealed; protoconch with more or less developed irregularly to densely spaced tubercles; teleococonch without or with closely to moderately spaced, weakly to well-developed radial ribs that are more prominent on last whorl, microsculpture of tiny projections or anastomosing ridglets plus widely spaced, short periostracal setae, often lost in adults; whorls narrowly winding, separated by deep suture; body whorl slightly to moderately descending, periphery well rounded. Shell colour uniform, yellowish brown to brown. Lip of aperture strongly expanded, basal and palatal edges curved; outer palatal node weak to conspicuously thickened internally, basal node absent to prominent, parietal wall inconspicuous or with thin callus.

Radula: 1–2 mm long; C + 6–8 + 2–3 + 10–14.

Genital anatomy: Penis without penial sheath, with well-developed, reflected or winding epiphallus with minute to short flagellum. Inner penial wall supporting two to four, more or less developed longitudinal pilasters. Penial retractor muscle attached at epiphallus near connection with penial complex. Epiphallus opens to penial lumen through simple, wide vergic ring. Vas deferens entering epiphallus terminally. Bursa copulatrix extending anterior end of spermoviduct, mostly S-folded.

Aestivation Strategy

Free sealer (modified after Solem, 1985a).

Comparative Remarks

Species of *Baudinella* are readily distinguished from all other Kimberley camaenids except *Setobaudinia* and **Molema** (see above for comparison with **Molema**) by their small size, discoid shell, wide umbilicus, occasional presence of periostracal setae (at least in juve-

TABLE 8. Shell parameters of *Baudinella* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens.

Species	N	Height (H)	Diameter (D)	Whorls	H/D Ratio
B. thielei n. sp.	13	2.8–3.3 (3.1 ± 0.2)	6.8–7.3 (7.1 ± 0.1)	3.1–3.3 (3.2 ± 0.1)	0.39–0.47 (0.43 ± 0.02)
B. boongareensis n. sp.	11	2.8–3.5 (3.0 ± 0.2)	6.6–7.5 (7.0 ± 0.3)	3.0–3.5 (3.2 ± 0.1)	0.38–0.47 (0.43 ± 0.03)
B. tuberculata n. sp.	15	3.1–3.8 (3.5 ± 0.2)	6.5–7.3 (6.8 ± 0.2)	3.1–3.5 (3.8 ± 0.1)	0.48–0.55 (0.51 ± 0.02)
B. setobaudinioides n. sp.	11	2.8–3.6 (3.1 ± 0.3)	6.7–7.6 (7.0 ± 0.3)	2.9–3.6 (3.2 ± 0.2)	0.41–0.51 (0.44 ± 0.03)
B. occidentalis n. sp.	16	2.5–3.2 (2.9 ± 0.2)	6.1–7.0 (6.6 ± 0.3)	3.0–3.4 (3.2 ± 0.1)	0.40–0.46 (0.43 ± 0.02)

niles), and strongly reflected, thick apertural lip with curved edges. *Setobaudinia* species are very similar in shell shape and size and cannot be readily distinguished from *Baudinella* by means of their shell. Solem (1985a), who knew only two *Baudinella* species, stated that shells essentially differ from *Setobaudinia* by presence of radial ribs and by prominence of nodes of apertural lip. However, some *Baudinella* species have very weak or no axial ribs and several have only weakly developed nodes, which do not differ from those found in *Setobaudinia*. Rather, shells differ microscopically in that radial growth lines or even ribs are present in *Baudinella* but much weaker or absent in *Setobaudinia*. Usually, *Setobaudinia* exhibits a regular pattern of radially arranged periostracal projections not found in *Baudinella*. Many *Baudinella* species have a more strongly reflected apertural lip, but this feature is not diagnostic for all species. Most reliably, the genera can be differentiated by their genital anatomy. Important key features are shorter bursa copulatrix extending anterior end of spermoviduct (reaching anterior end of albumen gland in *Setobaudinia*), absence of penial verge and lateral lamellae of interior penial wall (present in *Setobaudinia*).

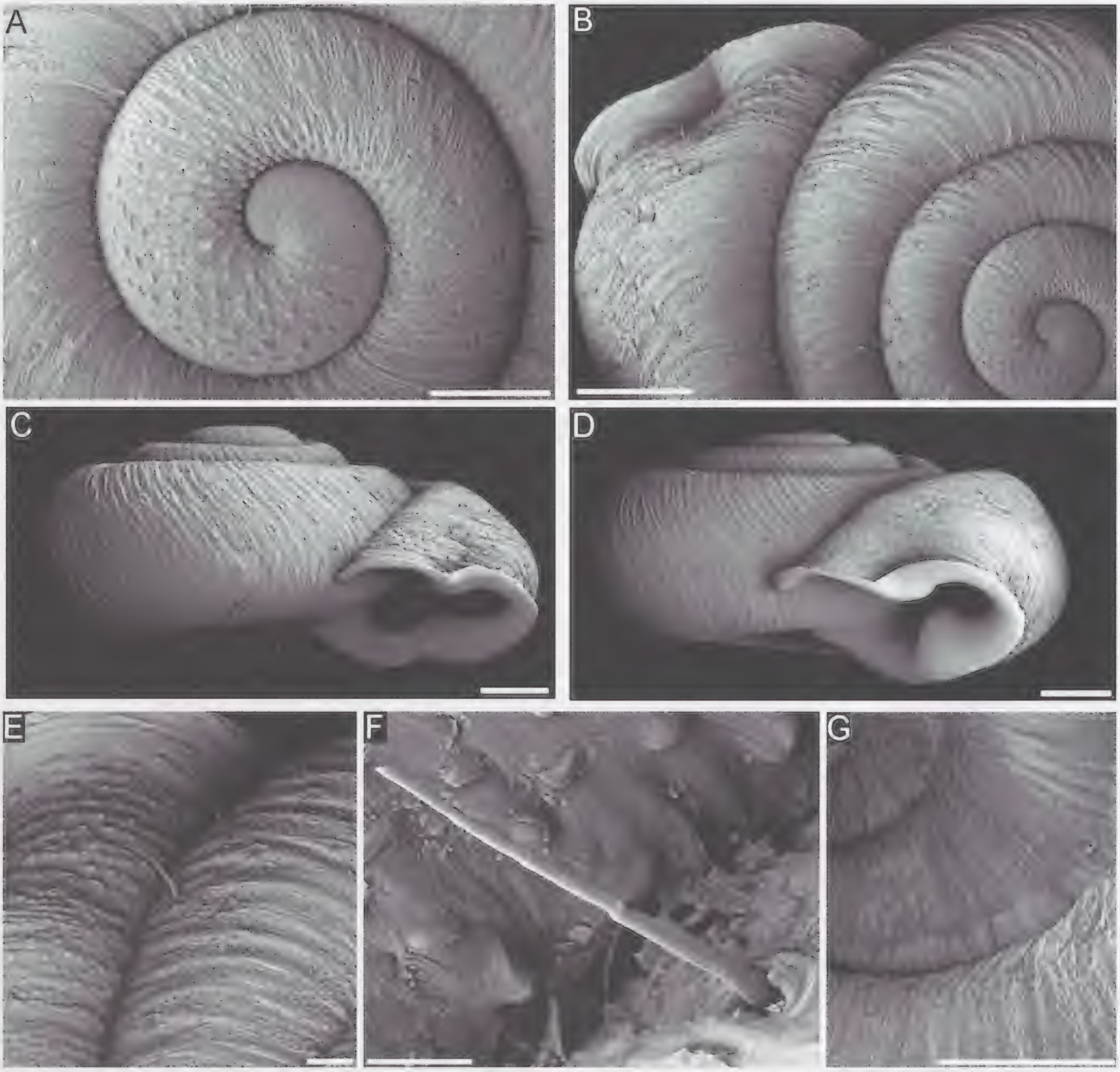

FIG. 106. SEM micrographs of shells of ***Baudinella thielei*** n. sp. paratype AM C471738 (Bigge Island). A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Lateral view of last whorl; D: Lateral view on aperture showing dentition. Scale bars B–D = 1 mm; E: Detail of sculpture on last whorl behind aperture, viewed from above. Scale bar = 200 µm; F: Close-up of periostracal hair. Scale bar = 50 µm; G: Inner umbilical whorls. Scale bar = 500 µm.

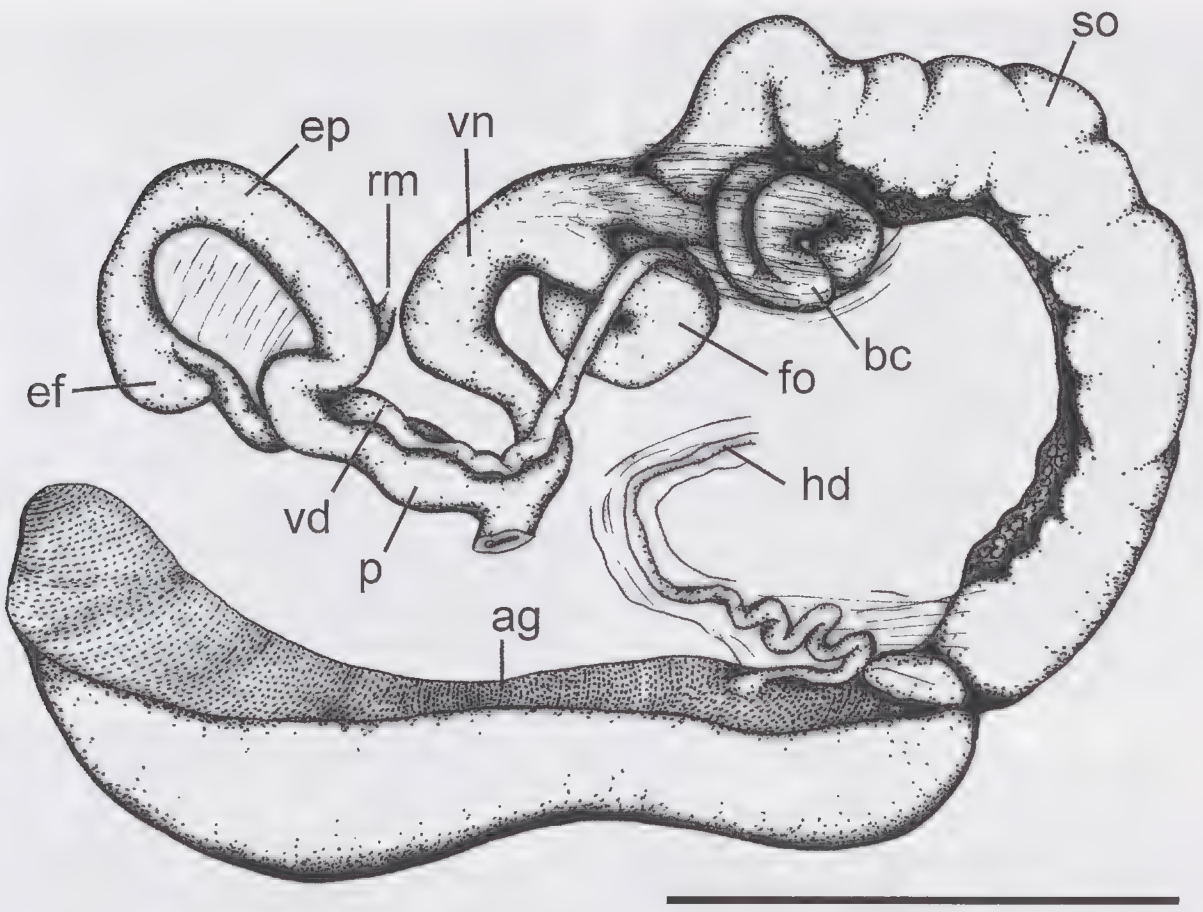

FIG. 107. Genital anatomy of ***Baudinella thielei*** n. sp. holotype WAM S58442 (Bigge Island, July). Scale bar = 2 mm.

Diversity and Distribution (Fig. 102)

Next to the type species, *B. baudinensis* from Baudin Island, Admiralty Gulf, Solem (1985a) described a second species from the Prince Regent Reserve. Solem (1991) listed two undescribed taxa from coastal localities in the York Sound, Prince Frederick Harbour and Bigge Island. Here five new species are being described from Bigge (previously listed as undescribed), Boongaree, Augustus, Coronation and D'Arcy islands, respectively.

Baudinella thielei n. sp.

Figs. 79N, 106–108

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Bigge Island, 14°35'33"S, 125°11'19"E; coll. Michael Shea, 27/07/2007, KIS 1–5 (S-facing slopes, mixed eucalyptus and dry vine thicket on sandstone scree, northern side of a creek valley; aestivating in soil under litter).

Material Examined

Holotype WAM S58442 (preserved specimen, dissected). Paratypes WAM S36756 (4 preserved specimens), WAM S36397 (15 shells); WAM S36394 (8 shells) from 14°35'20"S, 125°11'07"E; WAM S36395 (shell) from 14°35'27"S, 125°11'03"E; WAM S36396 (20 shells), AM C471737 (14 shells) from 14°35'16"S, 125°11'06"E; WAM S36398 (15 shells, 5 preserved specimens) from 14°35'16"S, 125°11'02"E; WAM S36975 (50 shells), AM C471738 (28 shells) from 14°35'16"S, 125°11'02"E; WAM S36399 (shell)

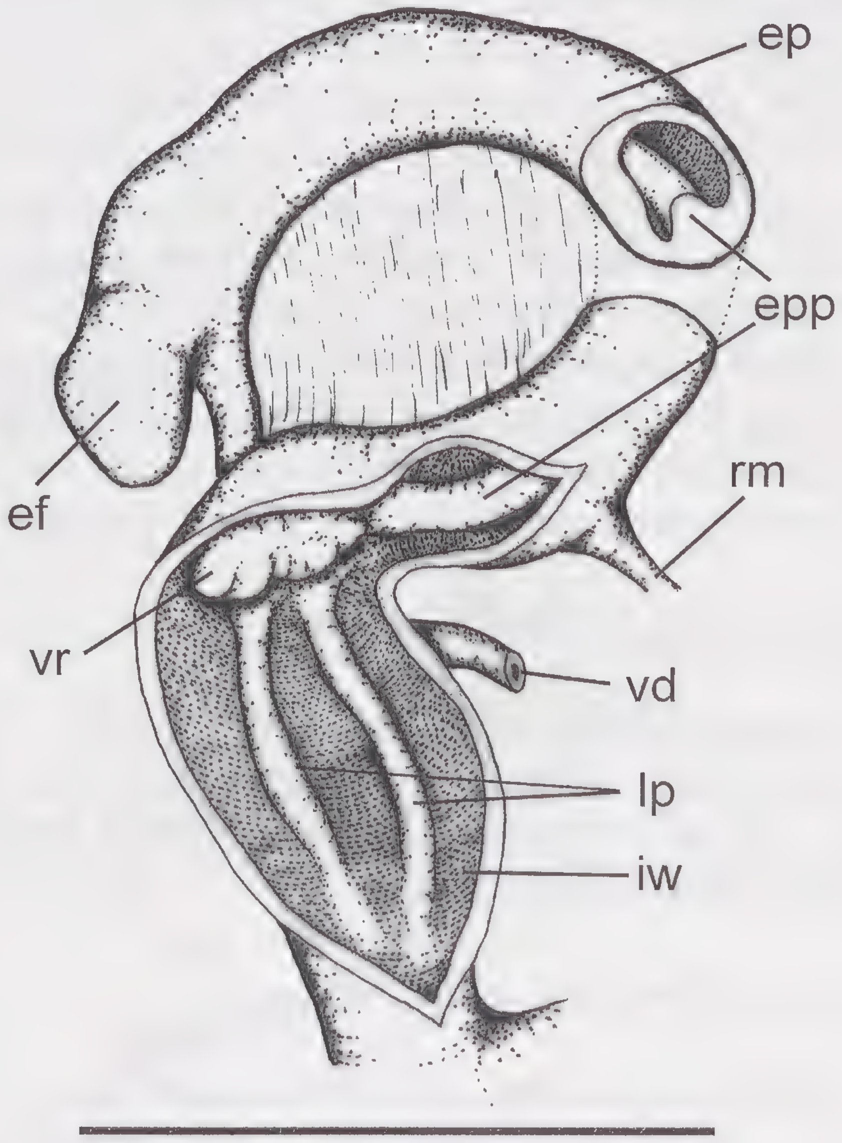

FIG. 108. Penial anatomy of ***Baudinella thielei*** n. sp. holotype WAM S58442 (Bigge Island, July). Scale bar = 1 mm.

from 14°35'19"S, 125°11'08"E; WAM S36400 (7 shells) from 14°35'10"S, 125°11'06"E; WAM S36900 (preserved specimen) from 14°35'15"S, 125°11'05"E.

Etymology

Named in honour of Johannes Thiele, former curator of Mollusca at the Museum of Natural History, Berlin, who named this genus; noun in genitive case.

Description

Shell (Figs. 79N, 106): Small (D = 7.1 mm on average, Table 8), with low spire. Protoconch with well developed, radially arranged, densely spaced, comparatively large tubercles; extending < 1 whorl. Teleoconch with narrowly spaced, indistinct to fine radial ribs (most prominent on first whorl and base of shell), and microsculpture of tiny projections, irregularly spaced, thin and short periostracal hairs may be present, but mostly worn in adults. Lip of aperture strongly expanded and reflected, thickened; outer palatal node conspicuously thickened, basal node well developed, parietal wall with thin callus.

Genital anatomy (Figs. 107–108): Penis comparatively short (clearly shorter than vagina). Epiphallus comparatively long (much longer than penis), reflected, supporting a short but comparatively wide epiphallic flagellum at distal end of epiphallus; inner epiphallic wall supporting one well-developed longitudinal pilaster. Inner penial wall supporting two rather weak longitudinal pilasters, most prominent at posterior part of inner wall, tapering anteriorly. Vagina elongate, winding. Bursa copulatrix extending anterior end of spermoviduct, head heavily coiled, attached to base of spermoviduct by connective tissue.

Mitochondrial Differentiation

Infraspecific genetic divergence: 0.007 (2 sequences); interspecific distances with respect to all other congeners: 0.133–0.160 (8 sequences, 3 species).

Comparative Remarks

Identical with "*Baudinella* NSP8" listed by Solem (1991) from Bigge Island and adjacent mainland. Most similar to *Baudinella baudinensis* and *B. regia* in having radial ribs and well-developed nodes at apertural lips but differs by more indistinct, closely spaced axial ribs. Typical for the present species is presence of two logitudinal penial pilasters. In addition, genetalia differ most conspicuously by presence of only one epiphallic pilaster and by heavily coiled head of bursa copulatrix.

Distribution (Fig. 102)

Bigge Island, in vine thickets; occurrence on adjacent mainland as mentioned by Solem (1991) awaits confirmation by comparative study of suitable material.

Baudinella boongareensis n. sp.

Figs. 79O, 109–111

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04'00"S, 125°11'11"E; coll. Michael Shea, 10/08/2007, KIS 1–34 (patches of vine thicket on W-facing dolerite slopes, talus; in soil under rocks and litter).

Material Examined

Holotype WAM S58443 (preserved specimen, dissected). Paratypes WAM S36747 (6 preserved specimens), AM C471739 (3 preserved specimens), WAM S36390 (5 shells), WAM S36391 (29 shells) from type locality; AM C471741 (3 preserved specimens), WAM S36743 (8 preserved specimens), AM C471740 (17 shells), WAM S36387 (40 shells), WAM S36388 (88 shells) from 15°04'31"S, 125°11'07"E; WAM S36386 (3 shells) from 15°04'21"S, 125°11'06"E; AM C471742 (15 preserved specimens), WAM S36744 (24 preserved specimens) from 15°04'36"S, 125°11'12"E; WAM S36745 (7 preserved specimens) from 15°04'15"S, 125°11'14"E; WAM S36746 (10 preserved specimens), WAM S36389 (21 shells) from 15°04'08"S, 125°11'05"E; WAM S36392 (9 shells) from 15°04'36"S, 125°11'18"E; WAM S36393 (9 shells) from 15°04'33"S, 125°10'58"E; WAM S37686 (6 preserved specimens) from 15°04'30"S, 125°11'21"E; WAM S37687 (5 preserved specimens), WAM S49054 (2 shells) from 15°04'19"S, 125°11'18"E.

Etymology

In reference to the type locality, Boongaree Island; adjective of feminine gender.

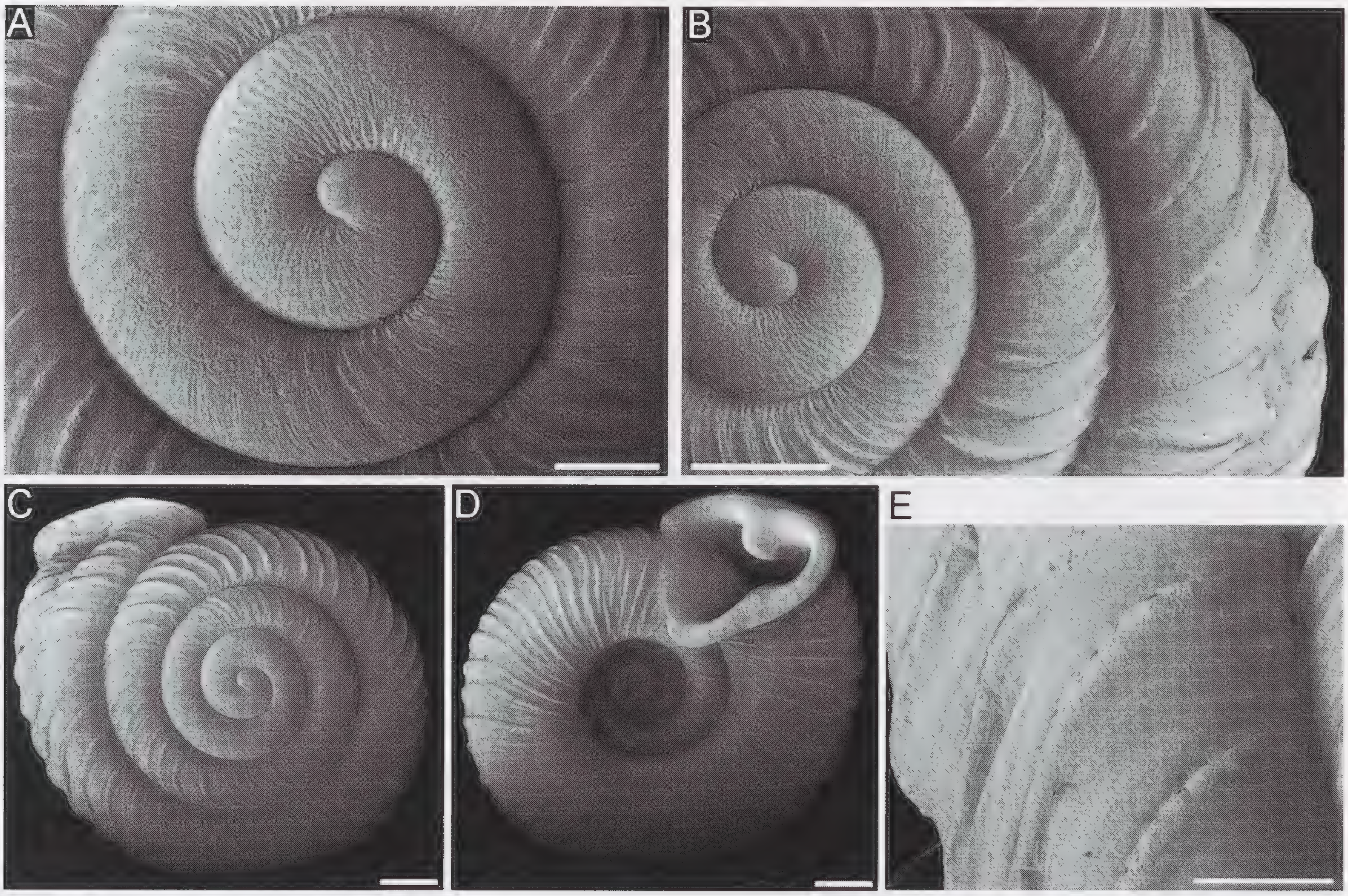

FIG. 109. SEM micrographs of shells of ***Baudinella boongareensis*** n. sp. paratype AM C471740 (Boongaree Island). A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Entire shell viewed from below showing umbilicus and aperture with dentition. Scale bars B–D = 1 mm; E: Detail of sculpture on last whorl behind aperture, viewed from above. Scale bar = 500 µm.

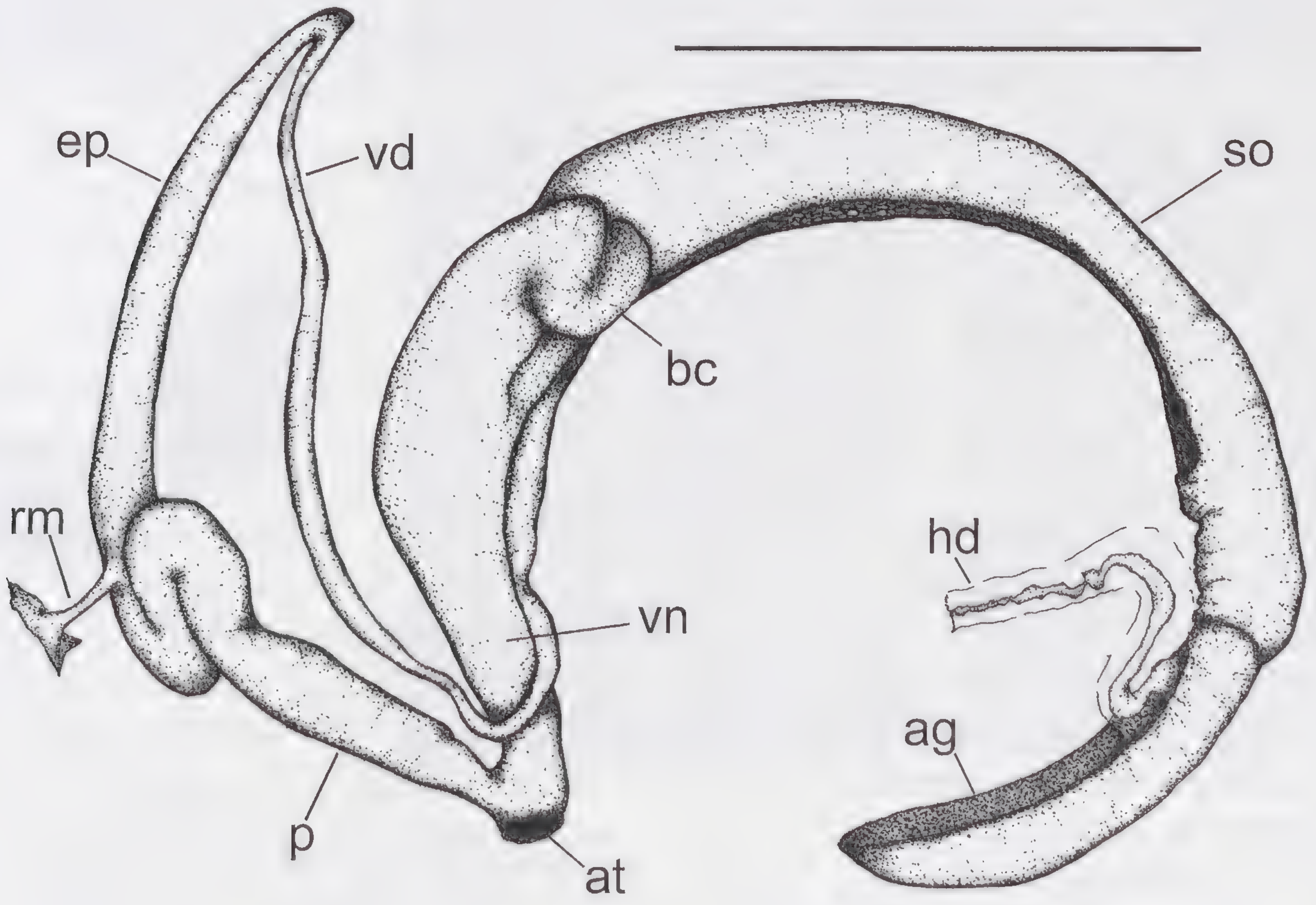

FIG. 110. Genital anatomy of ***Baudinella boongareensis*** n. sp. holotype WAM SS58443 (Boongaree Island, August). Scale bar = 3 mm.

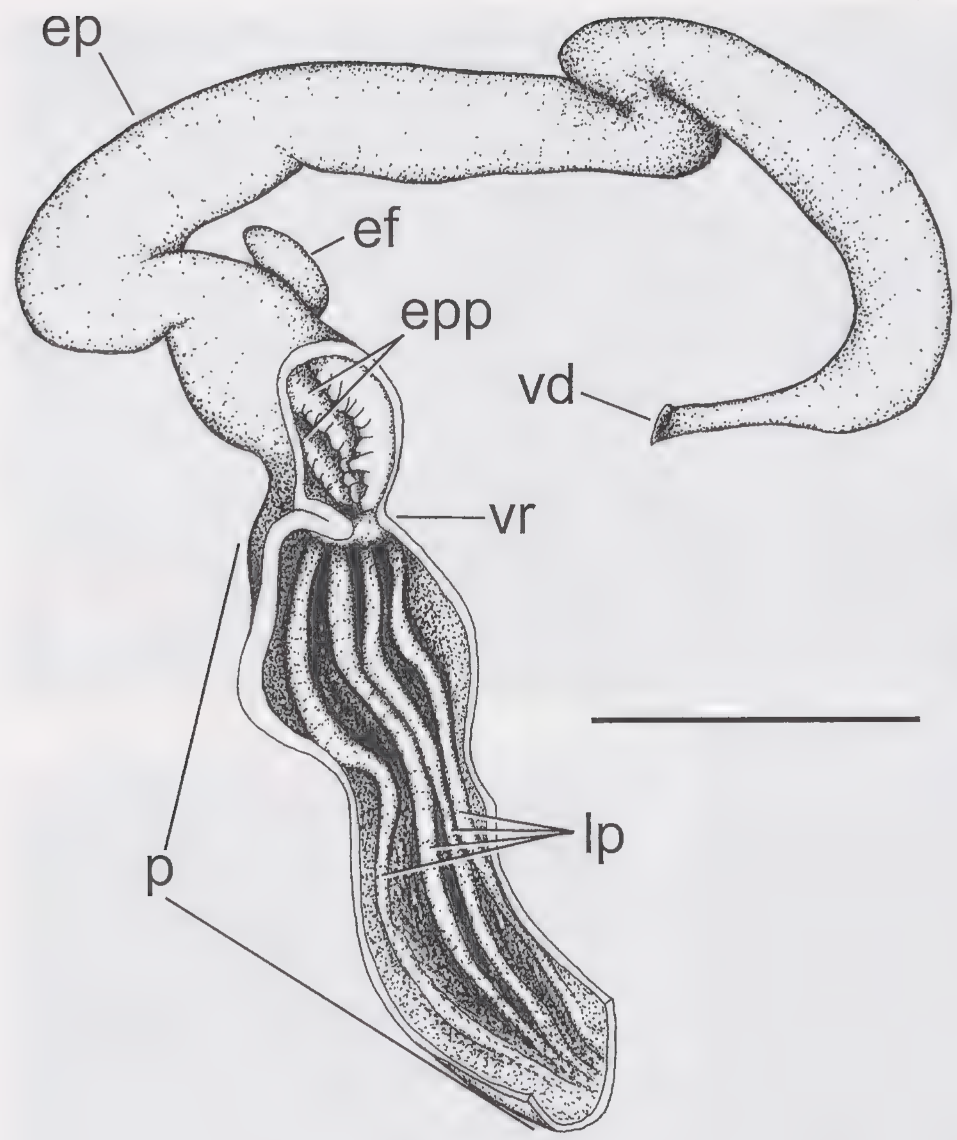

FIG. 111. Penial anatomy of ***Baudinella boongareensis*** n. sp. holotype WAM SS58443 (Boongaree Island, August). Scale bar = 1 mm.

Description

Shell (Figs. 79O, 109): Small (D = 7.0 mm on average, Table 8), with low spire. Protoconch with well developed, radially arranged, densely spaced tubercles; extending about one whorl. Teleoconch with widely spaced, very strong radial ribs (most prominent on first whorl and base of shell), very sparse and indistinct microsculpture of tiny projections, periostracal setae absent. Lip of aperture strongly expanded and reflected, thickened; outer palatal and basal nodes strongly developed, parietal wall callued.

Genital anatomy (Figs. 110–111): Penis elongate, straight. Epiphallus longer than penis, reflected, supporting a very short epiphallic flagellum near distal end; inner epiphallic wall supporting two longitudinal pilasters. Inner penial wall supporting four well-developed longitudinal pilasters along entire surface that taper anteriorly. Vagina about as long as penis. Bursa copulatrix extending anterior end of spermoviduct, head S-folded, attached to base of spermoviduct by connective tissue.

Comparative Remarks

Most similar to *B. baudinensis* in having strongly developed, widely spaced, radial ribs and very prominent nodes of apertural lip; differing essentially by development of penial wall pilasters. Shell differs from other congeners by strong, widely spaced radial ribs.

Distribution (Fig. 102)

Boongaree Island, in vine thickets.

Baudinella tuberculata n. sp.

Figs. 79P, 112–115

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, southern section of Coronation Island, 15°01’45”S, 124°56’49”E; coll. Vince Kessner, 1/06/2008, KIS 3–90 (vine thicket on lower and middle slopes, cliffs, scree; abundant under rocks in loose soil).

Material Examined

Holotype WAM S58444 (preserved specimen, dissected). Paratypes AM C471743 (43 preserved specimens), WAM S37062 (103 preserved specimens), AM C471744 (30 shells), WAM S37259 (68 shells) from type locality; AM C471745 (50 preserved specimens), WAM S37056 (100 preserved specimens), AM C471746 (49 shells), WAM S37253 (80 shells) from 15°01’47”S, 124°57’15”E.

Additional non-type material WAM S37256 (8 shells) from 15°01’42”S, 124°57’08”E; WAM S37057 (56 preserved specimens), WAM S37254 (62 shells) from 15°01’49”S, 124°57’17”E; WAM S37058 (27 preserved specimens), WAM S37255 (22 shells) from 15°01’52”S, 124°56’56”E; WAM S37059 (24 preserved specimens), WAM S37257 (12 shells) from 15°01’55”S, 124°56’59”E; WAM S37061 (48 preserved specimens), WAM S37258 (34 shells) from 15°01’27”S, 124°56’28”E; WAM S37063 (55 preserved specimens), WAM S37260 (8 shells) from 15°01’58”S, 124°57’21”E; WAM S37261 (14 shells) from 15°01’59”S, 124°57’15”E; WAM S37060 (6 preserved specimens) from 15°01’59”S, 124°56’53”E; AM C471747 (shell), WAM S49047 (2 shells) from Malby Island, northwest of Coronation Island, 14°57’00”S, 124°53’27”E.

Etymology

From “*tuberculum*” (Latin = small swelling); in reference to conspicuously fine tuberculation of the shell being typical for this species; adjective of feminine gender.

Description

Shell (Figs. 79P, 112A–E, 113): Small (D = 6.8 mm on average, Table 8), with moderately elevated spire. Protoconch with strongly developed, radially arranged tubercles; extending about one whorl. Teleoconch entirely covered with strongly developed, radially arranged tubercles, radial sculpture consisting of growth lines only, periostracal setae and radial ribs absent. Lip of aperture expanded and reflected,

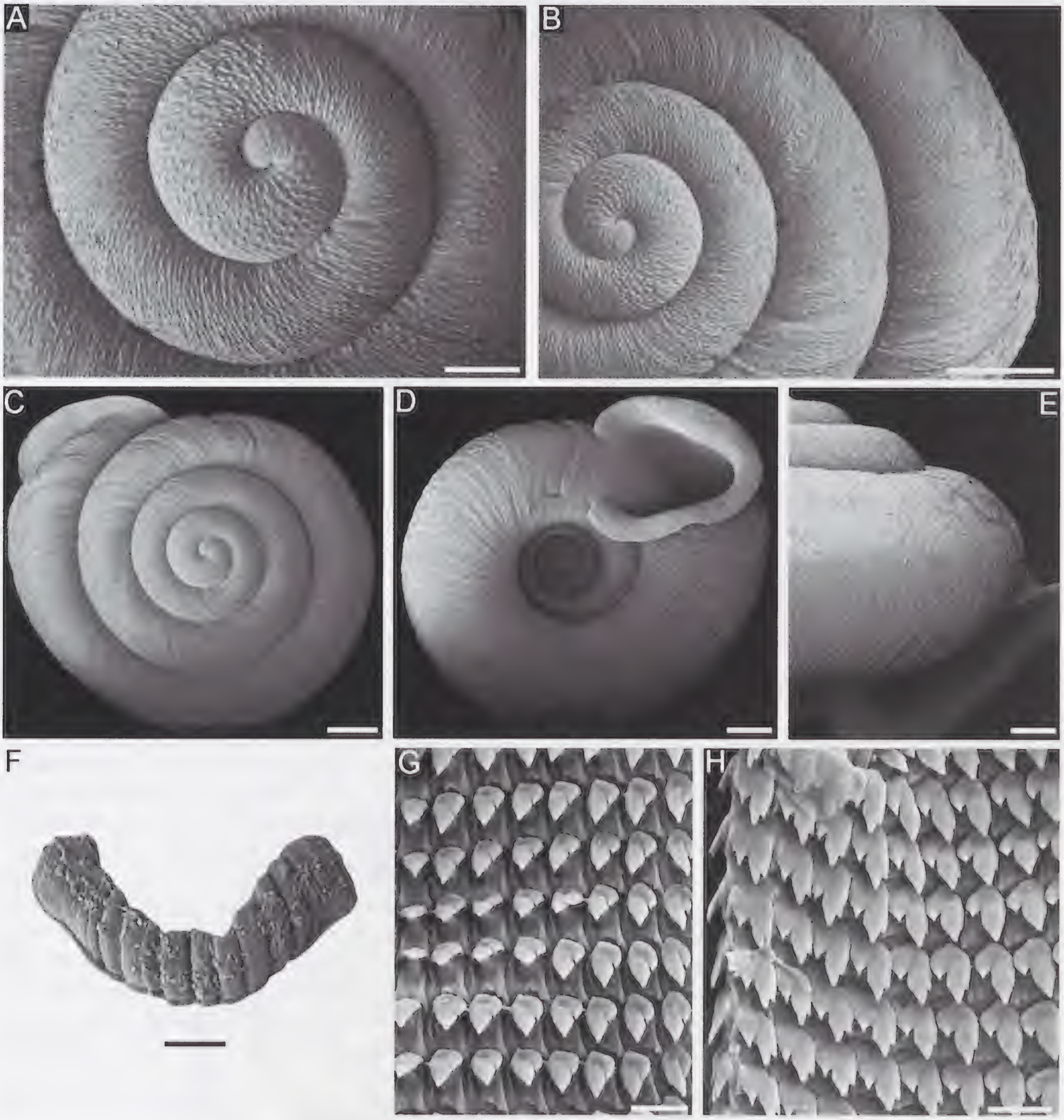

FIG. 112. SEM micrographs of ***Baudinella tuberculata*** n. sp. (Coronation Island). A–E: Shell paratype AM C471746. A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Entire shell viewed from below showing umbilicus and aperture. Scale bars B–D = 1 mm; E: Detail of sculpture on last whorl, lateral view. Scale bar = 500 µm; F: Jaw paratype AM C471743. Scale bar = 100 µm; G–H: Radula paratype AM C471743. Scale bars = 20 µm; G: Central and inner lateral teeth viewed from above; H: Transitional and middle marginal teeth viewed from above.

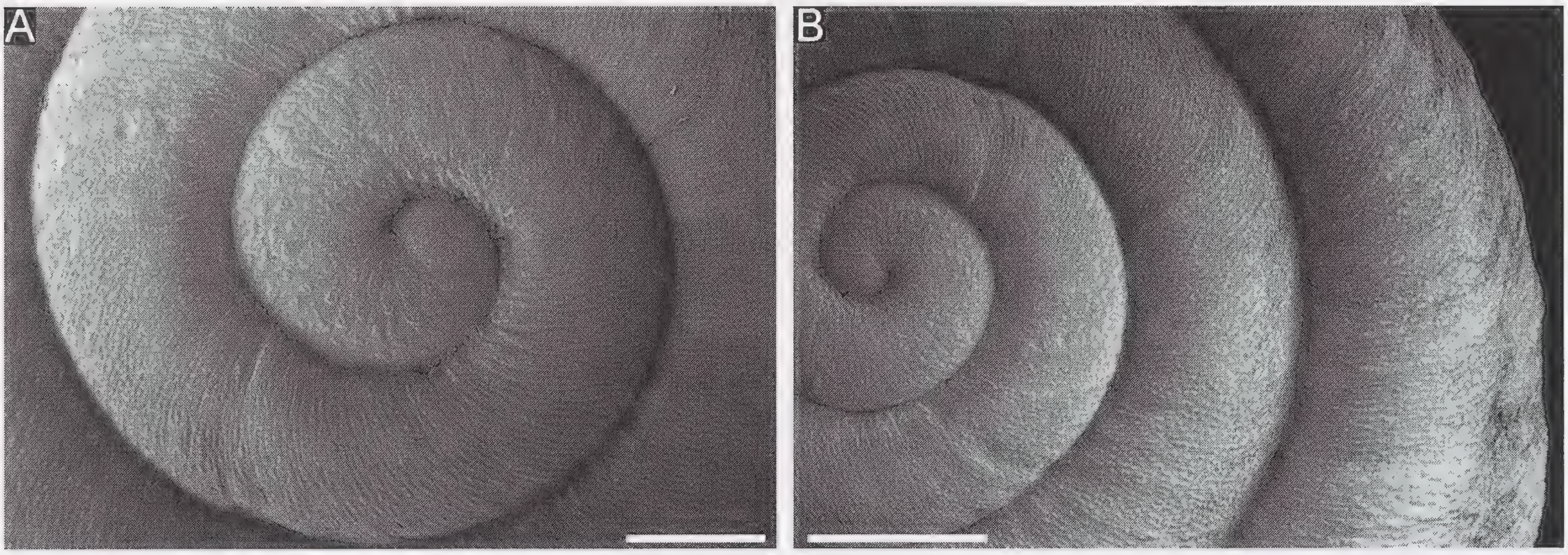

FIG. 113. SEM micrographs of the shell of ***Baudinella tuberculata*** n. sp. (AM C471747, Malby Island). A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above. Scale bar = 1 mm.

thickened; outer palatal and basal nodes very weakly developed, parietal wall inconspicuous.

Digestive anatomy (Fig. 112F–H): Jaw consisting of 14–15 plates (n = 1). Radula 1–2 mm long, C + 7–8 + 2–3 + 13–14 (n = 2).

Genital anatomy (Figs. 114–115): Penis elongate with slightly inflated proper. Epiphallus well developed, longer than penis, reflected, supporting well-developed epiphallic flagellum; inner epiphallic wall supporting two longitudinal pilasters. Inner penial wall supporting two well-developed, distinct longitudinal pilasters along entire surface tapering anteriorly. Vagina strongly elongated, tubular, longer than penis and much longer than free oviduct. Bursa copulatrix short, extending anterior end of spermoviduct, head S-folded, attached to base of spermoviduct by connective tissue.

Mitochondrial Differentiation

Infraspecific genetic divergence: 0.0–0.011 (3 sequences); interspecific distances with respect to all other congeners: 0.133–0.160 (7 sequences, 3 species).

Comparative Remarks

Differs from all other species by conspicuous, tuberculate microsculpture of shell, most

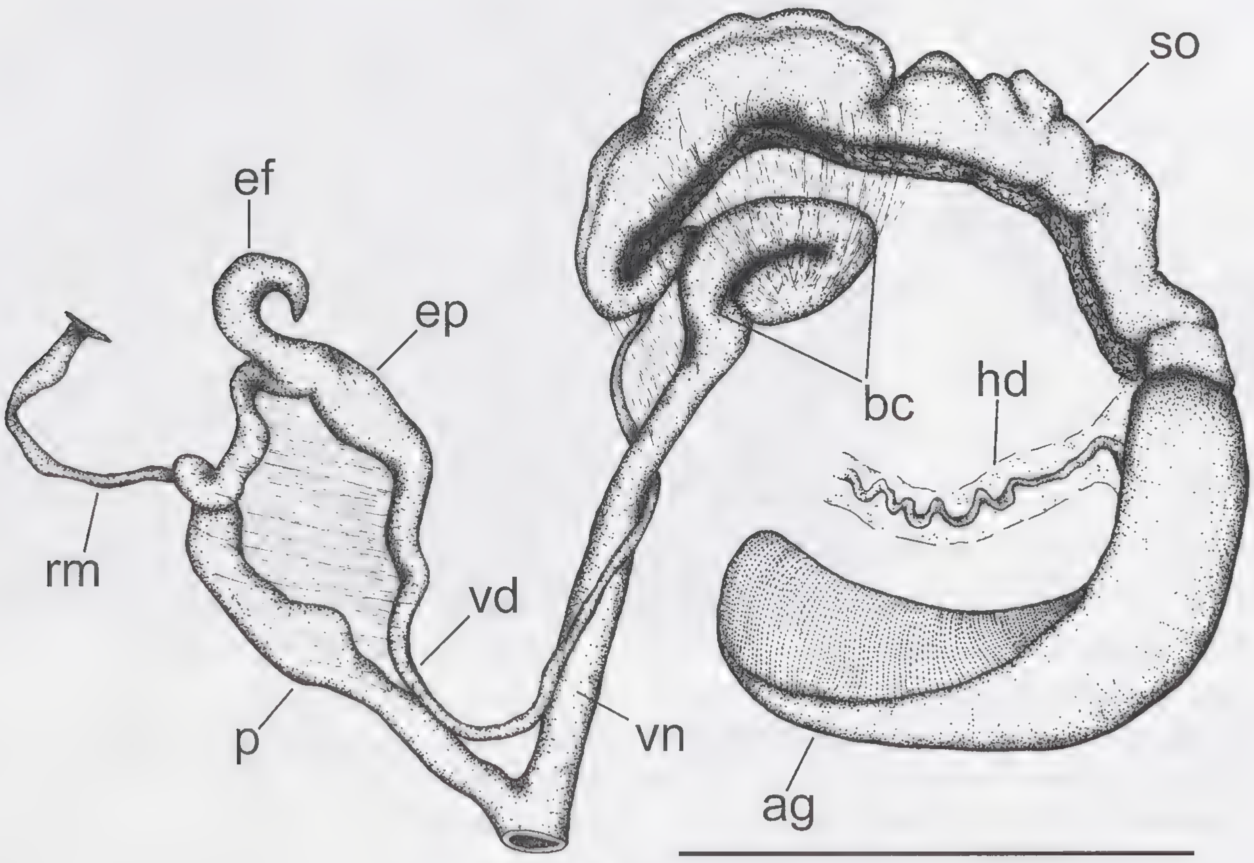

FIG. 114. Genital anatomy of ***Baudinella tuberculata*** n. sp. holotype WAM S58444 (Coronation Island, June). Scale bar = 3 mm.

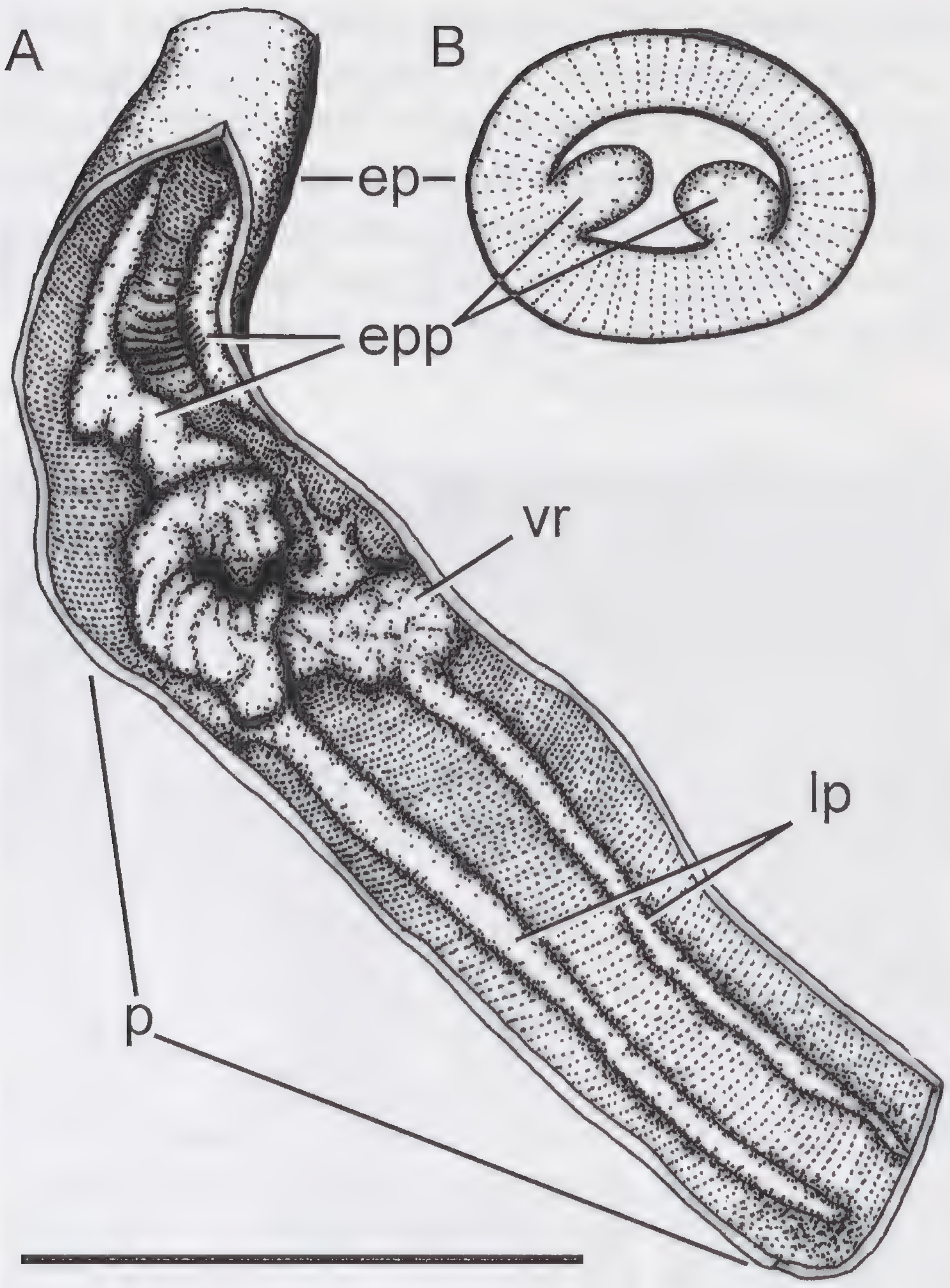

FIG. 115. Penial anatomy of ***Baudinella tuberculata*** n. sp. holotype WAM S58444 (Coronation Island, June). A: Penial anatomy; B: Schematic cross-section through epiphallus. Scale bar = 1 mm.

strongly elevated spire, and largest H/D ratio (Table 8). Inner penial wall supporting two instead of four longitudinal pilasters as found in ***B. boongareensis***. The relatively weak development of apertural nodes and absence of strong radial ribs were previously thought to be diagnostic for *Setobaudinia* (Solem, 1985a, 1991). Differs from ***Setobaudinia garlinju*** from Coronation Island by smaller size, absence of radial ribs and periostracal setae and more pronounced reflection of apertural lip. Two specimens from Malby Island, about 15 km NW of type locality are considered conspecific although having weaker pustulation (Fig. 113).

Distribution (Fig. 102)

Southern part of Coronation Island (not found in the northern part), and Malby Island, about 15 km in northwesterly direction; in vine thickets.

Baudinella setobaudinioides n. sp.

Figs. 79Q, 116–118

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, NW section of Augustus Island, 15°21’05”S, 124°31’47”E; coll. Michael Shea, 22/05/2008, KIS 1–45 (W-facing slope of low sandstone escarpment, scattered vine thicket trees; under rocks in litter).

Material Examined

Holotype WAM S58445 (preserved specimen, dissected). Paratypes AM C471748 (6 preserved specimens), WAM S37035 (13 preserved specimens), WAM S37263 (17 shells) from type locality; WAM S37036 (12 preserved specimens), WAM S37264 (7shells) from 15°21’06”S, 124°31’48”E; AM C471749 (12 shells), WAM S37265 (20 shells) from 15°21’24”S, 124°31’39”E; WAM S37037 (4 preserved specimens), WAM S37266 (16 shells) from 15°20’16”S, 124°31’16”E; WAM S37038 (18 preserved specimens), WAM S37267 (8 shells) from 15°19’58”S, 124°31’01”E; AM C471750 (10 preserved specimens), WAM S37685 (18 preserved specimens) from 15°20’11”S, 124°31’10”E.

Etymology

Derived from the genus name *Setobaudinia* and the Greek suffix “-oides” (οειδες, an adjective suffix for nouns = like, resemble), for this species exhibiting shell features previously held diagnostic for *Setobaudinia*; adjective of feminine gender.

Description

Shell (Figs. 79Q, 116A–E): Small (D = 7.0 mm on average, Table 8), with low spire. Protoconch with relatively large, sparsely arranged tubercles; extending about one whorl. Teleoconch with regularly spaced but indistinctly developed, radial ribs or growth lines, most prominent on first whorl, microsculpture of dense and fine pustules; periostracal hairs may be present particularly in young specimens. Lip of aperture expanded and reflected, thickened; outer palatal well developed, basal node very weak, parietal wall inconspicuous.

Digestive anatomy (Fig. 116F–H): Jaw consisting of many plates (n = 1). Radula ~ 1 mm long, C + 5–6 + 2–3 + 10–12 (n = 1).

Genital anatomy (Figs. 117–118): Penis moderately long. Epiphallus well developed, about as long as penis, reflected, supporting a well-developed epiphallic flagellum; inner epiphallic wall supporting two longitudinal pilasters. Inner penial wall supporting three indistinct longitudinal pilasters that taper anteriorly. Vagina much shorter than penis, inflated. Bursa copulatrix clearly extending anterior end of spermoviduct, head weakly S-folded, attached to base of spermoviduct by connective tissue.

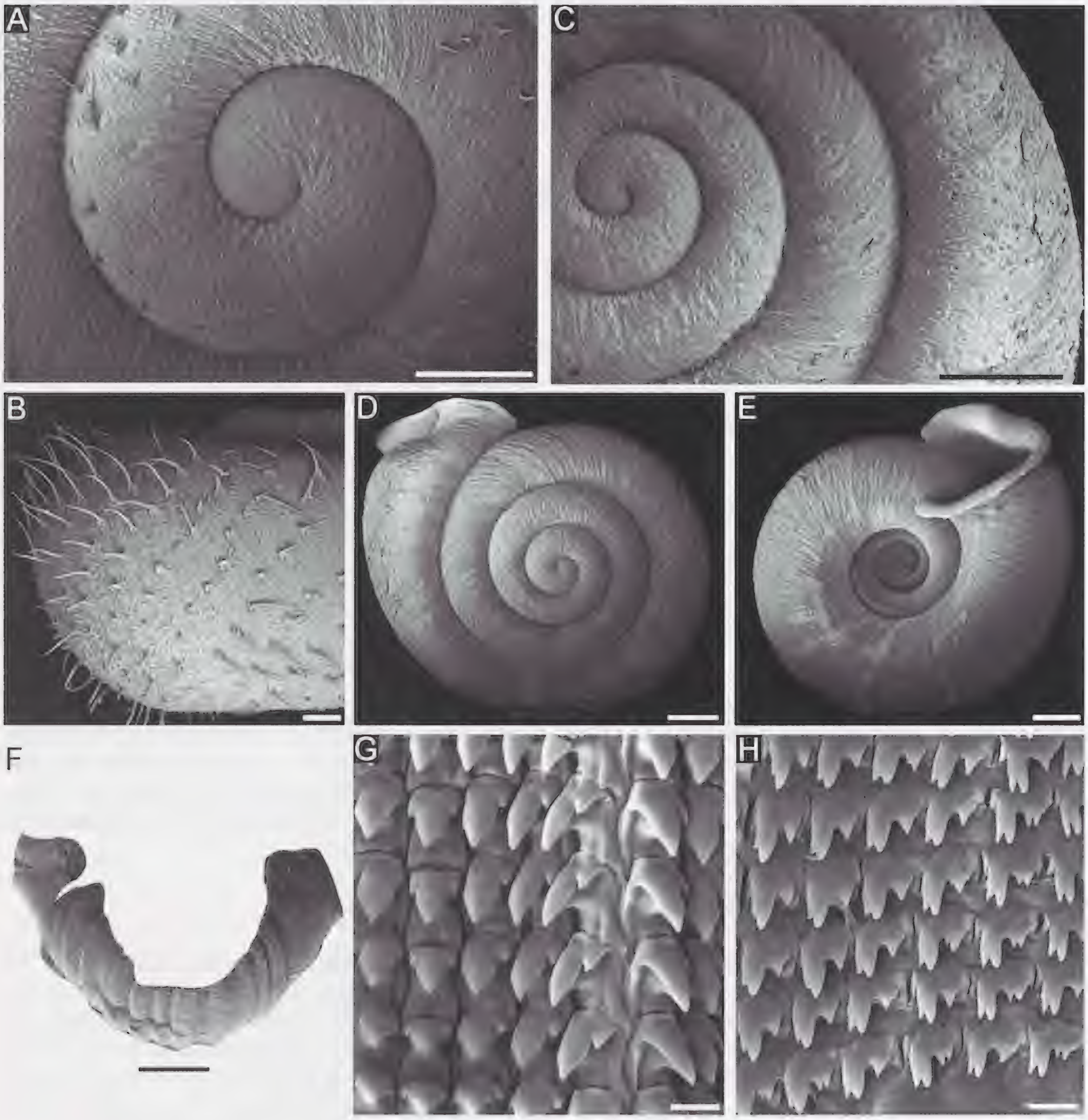

FIG. 116. SEM micrographs of ***Baudinella setobaudinioides*** n. sp. (Augustus Island). A–B: Shell paratype AM C471749 (juvenile shell with plenty of periostracal hairs). A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C–E: Shell paratype AM C471749 (adult shell without periostracal hairs); C: Entire shell viewed from above; D: Entire shell viewed from below showing umbilicus and aperture. Scale bars B–D = 1 mm; E: Detail of sculpture on last whorl, lateral view. Scale bar = 500 µm; F: Jaw paratype AM C471748. Scale bar = 100 µm; G–H: Radula paratype AM C471748. Scale bars = 20 µm; G: Central and inner lateral teeth viewed from above; H: Transitional and middle marginal teeth viewed from above.

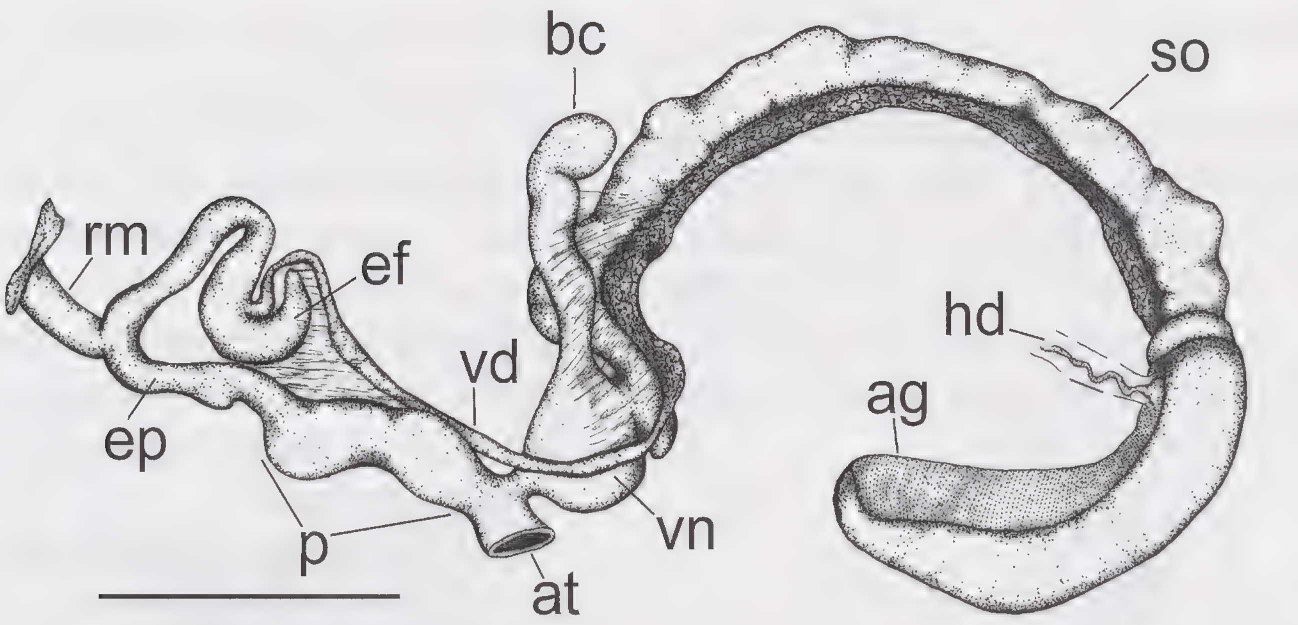

FIG. 117. Genital anatomy of ***Baudinella setobaudinioides*** n. sp. holotype WAM S58445 (Augustus Island, May). Scale bar = 2 mm.

Mitochondrial Differentiation

Infraspecific genetic divergence: 0.0 (2 sequences); interspecific distances with respect to all other congeners: 0.133–0.160 (8 sequences, 3 species).

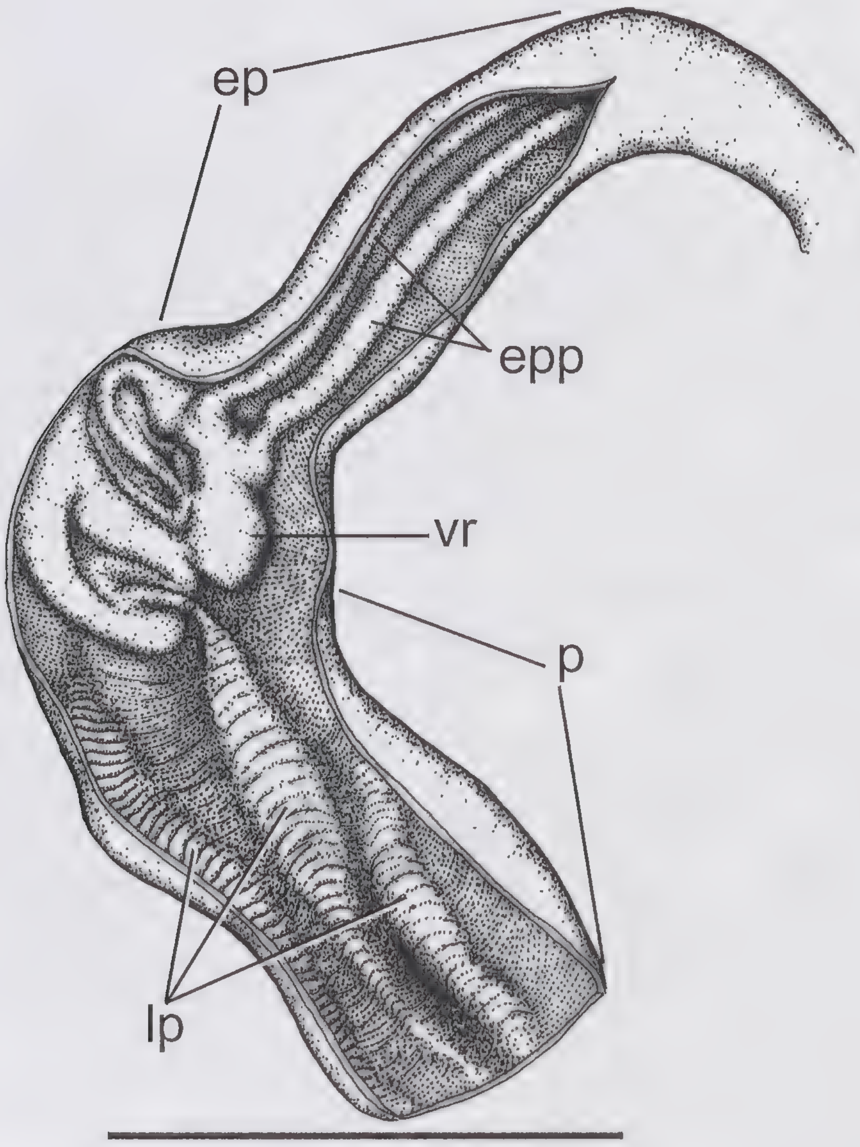

FIG. 118. Penial anatomy of ***Baudinella setobaudinioides*** n. sp. holotype WAM S58445 (Augustus Island, May). Scale bar = 1 mm.

Comparative Remarks

Differs from *B. baudinensis*, *B. regia* and ***B. boongareensis*** by weaker radial sculpture, weaker nodes of apertural lip and weaker reflection of apertural lip; from ***B. tuberculata*** by presence of ribs. Inner penial wall supporting three instead of four longitudinal pilasters like ***B. boongareensis***, or two like ***B. tuberculata***. The weak apertural nodes and absence of strong radial ribs were thought to be diagnostic for *Setobaudinia* (Solem, 1985a, 1991); material of this species was indeed mistaken as member of *Setobaudinia* as based on the shell. Shell differs from *Setobaudinia* essentially by smaller size. Radula differs from ***B. tuberculata*** by smaller size having fewer rows of teeth.

Distribution (Fig. 102)

Northwestern part of Augustus Island (not found in the southern part), in vine thickets.

Baudinella occidentalis n. sp.
Figs. 79R, 119–121

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, northwestern section of D’Arcy Island, 15°15’30”S, 124°25’57”E; coll. Roy Teale, 6/06/2008, KIS 2–58 (small vine thicket behind beach at base of very steep sandstone cliffs; under rocks).

Material Examined

Holotype WAM S58446 (preserved specimen, dissected). Paratypes WAM S37079 (5 preserved specimens), AM C471751 (2 shells), WAM S37262 (7 shells) from type locality; WAM S37694 (2 preserved specimens), AM C471752 (30 shells), WAM S49043 (57 shells) from 15°15'31"S, 124°25'58"E.

Etymology

From "*occidentalis*" (Latin = western) in reference to the fact that this species is at the western-most fringe of the currently known range of *Baudinella*; adjective of feminine gender.

Description

Shell (Figs. 79R, 119): Small (D = 6.6 mm on average, Table 8), with flat to low spire. Protoconch with relatively large, sparsely arranged tubercles; extending about one whorl. Teleoconch with regularly spaced but not very prominent radial ribs, most prominent on first whorl, microsculpture of sparse fine pustules; periostracal hairs may be present particularly in young specimens. Lip of aperture expanded and reflected, thickened; outer palatal well developed, basal node very weak, parietal wall inconspicuous.

Genital anatomy (Figs. 120–121): Penis very short, with inflated proper. Epiphallus longer than penis, winding, supporting small epiphallic flagellum; inner epiphallic wall supporting three longitudinal pilasters. Inner penial wall supporting two well-developed longitudinal pilasters along entire surface that taper anteriorly. Vagina, tubular, elongated, about as long as free oviduct. Bursa copulatrix just extending anterior end of spermoviduct, head unfolded, attached to base of spermoviduct by connective tissue.

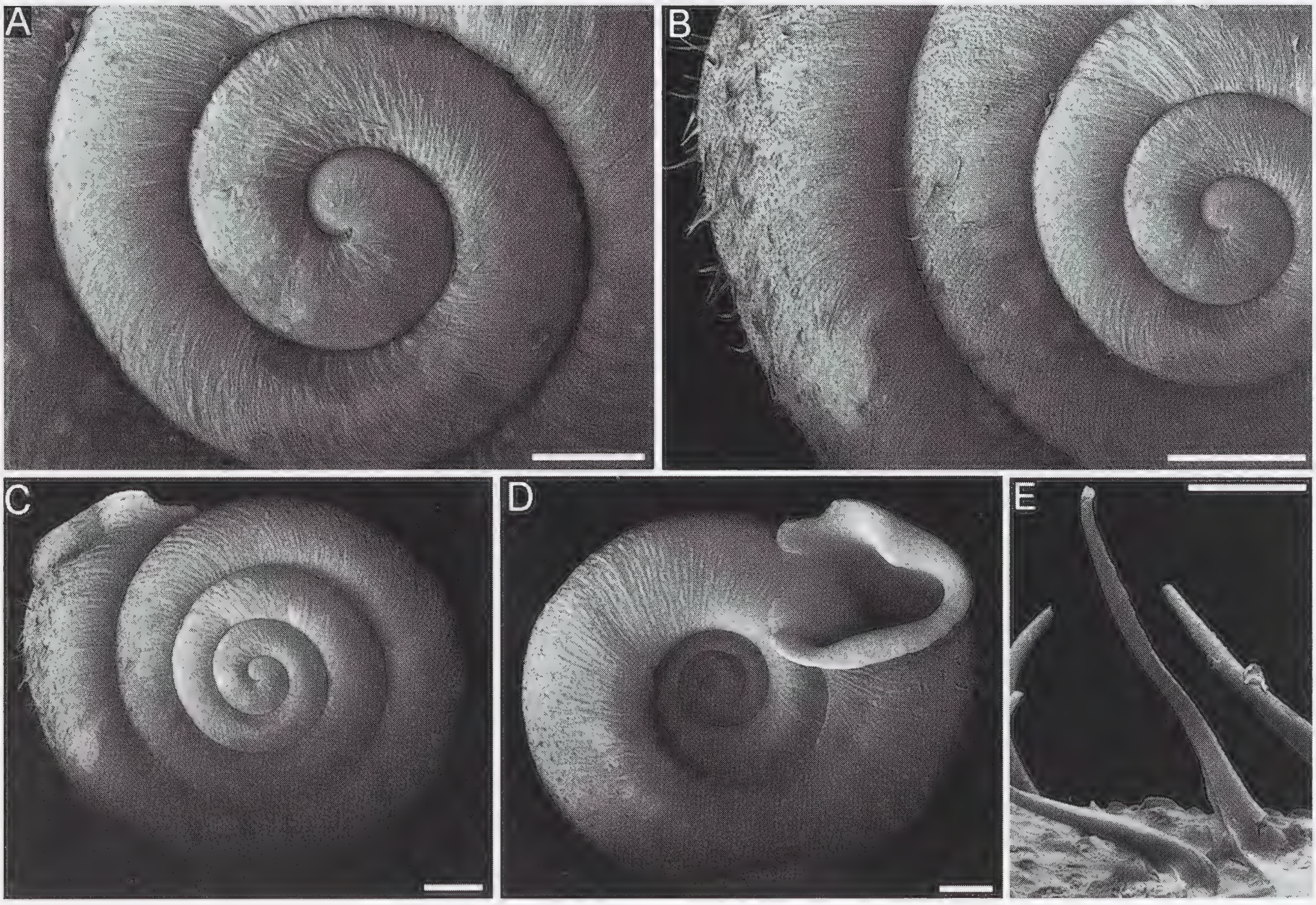

FIG. 119. SEM micrographs of the shell of ***Baudinella occidentalis*** n. sp. paratype AM C471751 (D'Arcy Island). A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Entire shell viewed from below showing umbilicus and aperture. Scale bars B–D = 1 mm; E: Close-up of periostracal hairs. Scale bar = 100 µm.

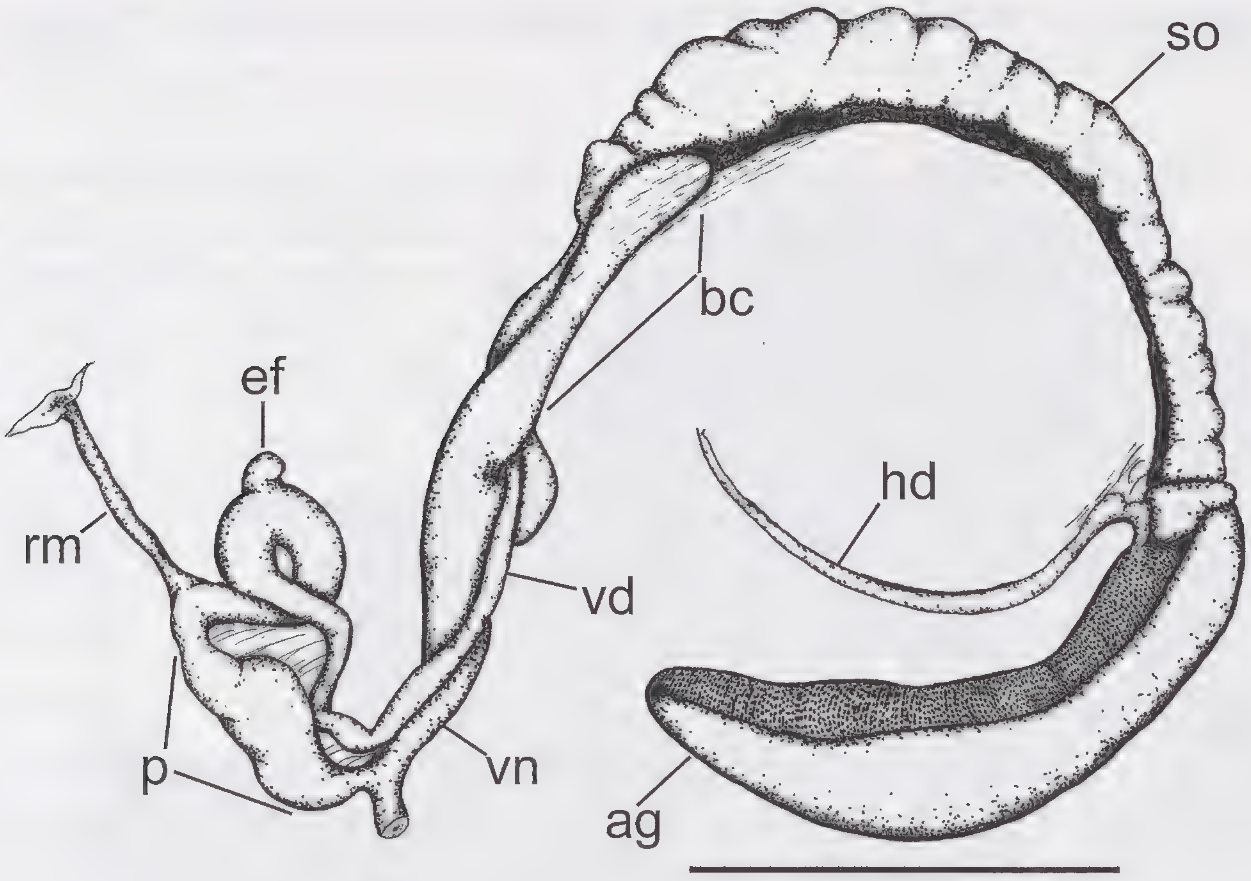

FIG. 120. Genital anatomy of **Baudinella occidentalis** n. sp. holotype WAM S58446 (D'Arcy Island, June). Scale bar = 3 mm.

Mitochondrial Differentiation

Infraspecific genetic divergence: 0.001–0.005 (3 sequences); interspecific distances with respect to all other congeners: 0.133–0.160 (7 sequences, 3 species).

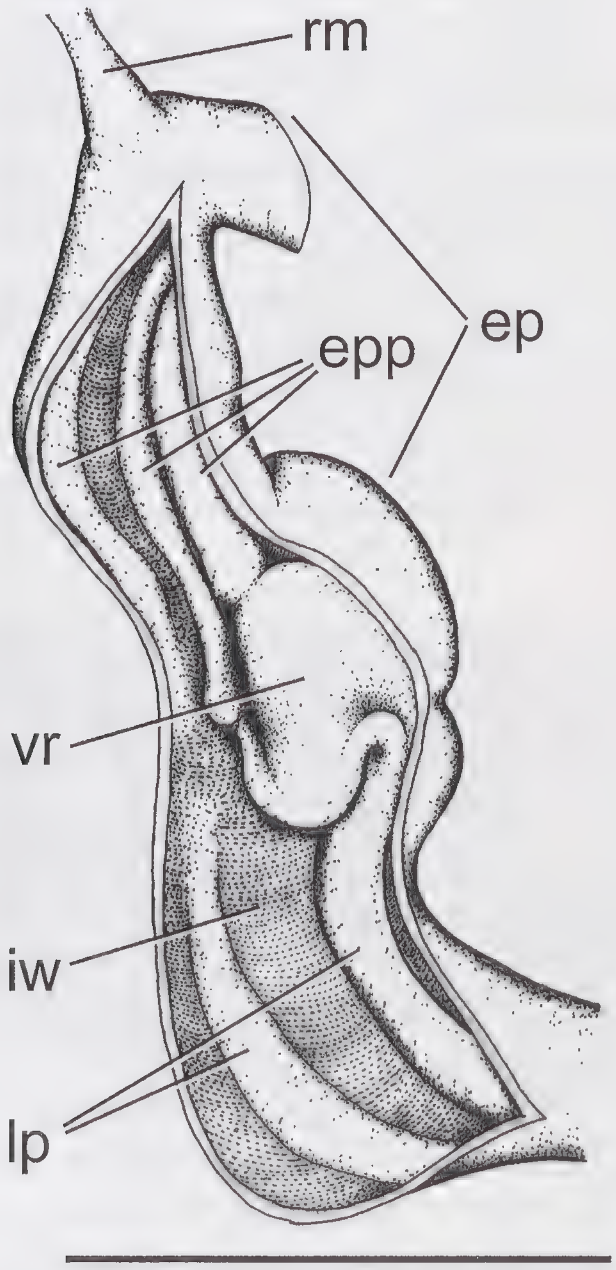

FIG. 121. Penial anatomy of **Baudinella occidentalis** n. sp. holotype WAM S58446 (D'Arcy Island, June). Scale bar = 1 mm.

Comparative Remarks

Smallest of all species treated here (Table 8). Most similar to ***B. setobaudinioides*** by presence of ribs. Inner penial wall supporting three instead of four longitudinal pilasters like ***B. boongareensis***, or two like ***B. tuberculata***. Relatively weak apertural nodes and absence of strong radial ribs were thought to be diagnostic for *Setobaudinia* (Solem, 1985a, 1991). Shell differs from *Setobaudinia* essentially by smaller size. Genital anatomy differs from all congeners most conspicuously by presence of three epiphallic pilasters.

Distribution (Fig. 102)

D'Arcy Island, in vine thickets.

Setobaudinia Iredale, 1933

Setobaudinia Iredale, 1933: 55; 1938: 109; 1939: 49–50; Solem, 1985a: 711–775; 1991: 202–207; Solem & McKenzie, 1991: 247–263. Type species: *Helix* (*Gonostoma*) *collingii* E. A. Smith, 1893, by original designation.

Taxonomic Remarks

The generic name was erected for the type species, *Helix* (*Gonostoma*) *collingii* E. A. Smith, 1893, from Parry Island, Admiralty

TABLE 9. Shell parameters of *Setobaudinia* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens.

Species	N	Height (H)	Diameter (D)	Umbilicus (U)	Whorls	H/D Ratio
S. rectilabrum	13	5.2–7.0 (6.1 ± 0.5)	11.2–13.8 (12.4 ± 0.7)	1.8–2.8 (2.1 ± 0.3)	3.7–4.2 (3.9 ± 0.1)	0.45–0.54 (0.50 ± 0.03)
S. herculea n. sp.	7	9.8–10.8 (10.3 ± 0.4)	18.3–20.5 (18.9 ± 0.7)	3.2–3.8 (3.5 ± 0.2)	4.6–4.7 (4.7 ± 0.0)	0.52–0.58 (0.54 ± 0.02)
S. ngurraali n. sp.	15	3.1–3.8 (3.4 ± 0.2)	6.7–7.8 (7.2 ± 0.4)	1.7–2.2 (1.9 ± 0.2)	3.0–3.6 (3.4 ± 0.2)	0.42–0.52 (0.48 ± 0.03)
S. umbadayi n. sp.	13	3.0–3.9 (3.5 ± 0.3)	6.5–8.0 (7.4 ± 0.4	1.5–2.5 (2.1 ± 0.3)	3.4–3.9 (3.6 ± 0.2)	0.43–0.49 (0.47 ± 0.02)
S. wuyurru n. sp.	10	3.5–4.5 (4.0 ± 0.3)	7.8–8.9 (8.5 ± 0.3)	2.0–3.0 (2.5 ± 0.4)	2.7–3.6 (3.4 ± 0.2)	0.44–0.53 (0.47 ± 0.02)
S. capillacea n. sp.	12	4.1–4.8 (4.4 ± 0.2)	8.3–9.2 (8.8 ± 0.3)	2.2–2.9 (2.5 ± 0.3)	3.5–4.2 (3.9 ± 0.2)	0.45–0.54 (0.50 ± 0.02)
S. garlinju n. sp.	14	3.5–4.6 (4.2 ± 0.3)	7.1–9.4 (8.3 ± 0.6)	1.7–2.2 (1.9 ± 0.2)	2.9–4.0 (3.5 ± 0.3)	0.48–0.53 (0.50 ± 0.02)
S. gumalamala n. sp.	11	3.5–4.2 (4.0 ± 0.2)	7.3–8.2 (7.7 ± 0.3)	1.9–2.1 (2.0 ± 0.1)	3.2–3.7 (3.5 ± 0.1)	0.48–0.57 (0.51 ± 0.02)
S. insolita n. sp.	12	3.8–4.6 (4.1 ± 0.2)	7.5–9.0 (8.3 ± 0.4)	1.7–2.5 (2.1 ± 0.3)	3.5–4.0 (3.6 ± 0.1)	0.45–0.54 (0.49 ± 0.03)
S. quinta n. sp.	17	3.0–4.0 (3.5 ± 0.3)	6.0–7.4 (6.7 ± 0.4)	1.3–2.0 (1.7 ± 0.2)	3.0–3.5 (3.2 ± 0.1)	0.47–0.60 (0.52 ± 0.03)
S. joycei n. sp.	13	3.8–4.8 (4.1 ± 0.2)	7.8–9.0 (8.3 ± 0.4)	2.1–2.7 (2.5 ± 0.2)	3.5–4.0 (3.7 ± 0.1)	0.44–0.61 (0.49 ± 0.04)
S. karczewski {XE ***"Setobaudinia karczewskiorum"***} n. sp.	2	3.3–4.0	8.0	2.3	3.3–3.5	0.49–0.50

Gulf (~ 14°19'23"S, 125°46'00"E), with data on its anatomy remaining unavailable. Solem (1985a) revised the taxonomy and described new species. Solem (1991) postulated fairly large ranges for some species, such as *S. collingii* and particularly *S. interrex* (Fig. 122). Based on emerging patterns of narrow range endemism in the Kimberley Camaenidae, I consider this assumption questionable. Since species identifications based only on shell characters are unreliable, the study of preserved material from various locations is required to elucidate species limits and ranges. Combined molecular phylogenetic and anatomical data provide evidence that species currently affiliated with *Damochlora* Iredale, 1938 (*Helix* (*Chloritis*) *rectilabrum* E. A. Smith, 1894), is a member of *Setobaudinia*. In fact, most, if not all, *Damochlora* species reveal anatomical features typical for *Setobaudinia*. *Damochlora* essentially differs by larger size, which might not be a suitable character to indicate generic distinctiveness. The taxonomic status of *Damochlora* with respect to *Setobaudinia* is pending to be resolved elsewhere through examination of its type species.

Diagnosis

Shell: Small to medium sized (D = 6.0–20.5 mm; Table 9), nearly discoidal with flat to moderately elevated spire; slowly increasing whorls separated by well-incised suture, umbilicus moderately to widely open, not concealed;

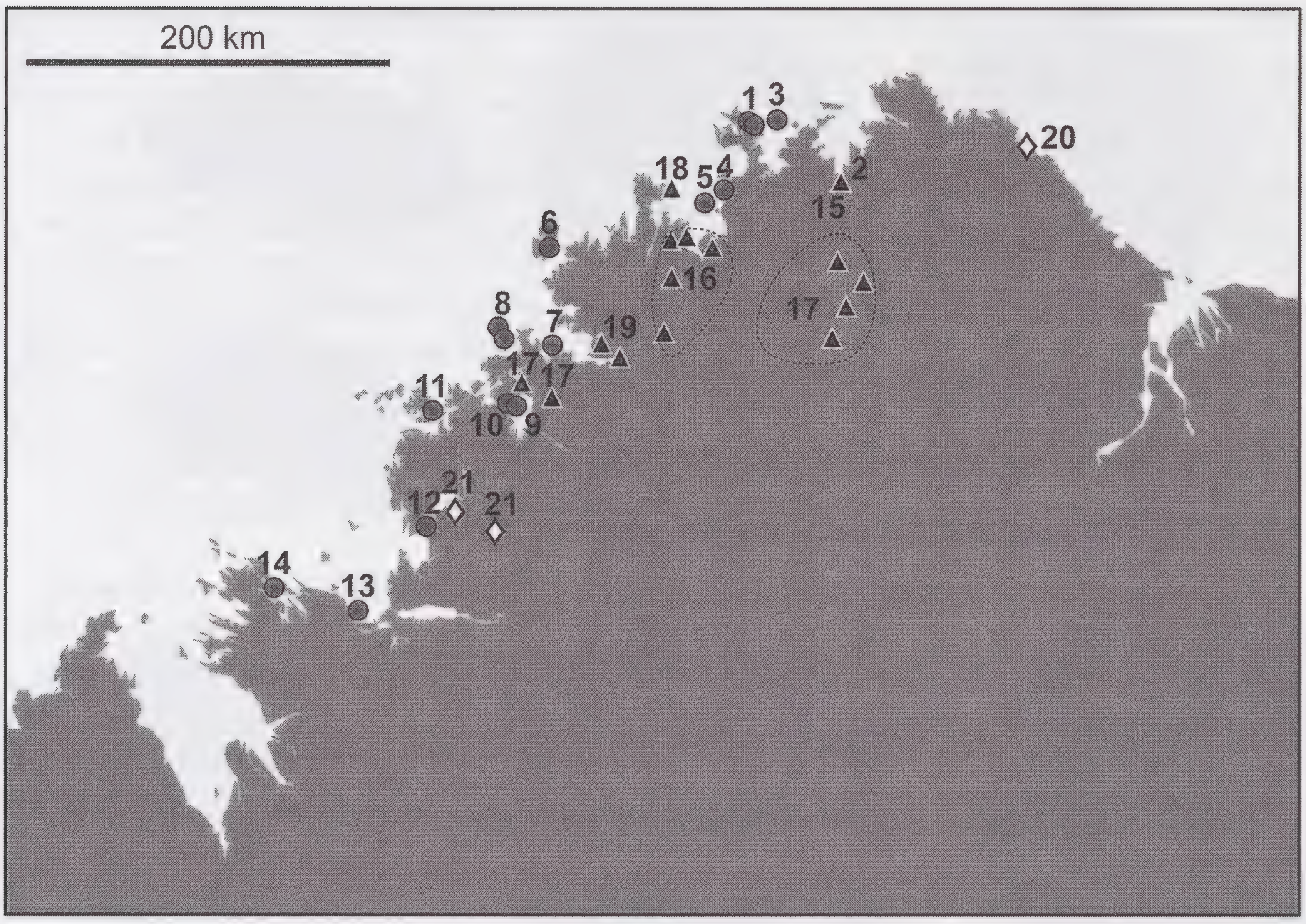

FIG. 122. Distribution map of *Setobaudinia* in the Kimberley. Circles = records of species treated herein: 1: *Setobaudinia rectilabrum* (Bougainville Peninsula, Wargul Wargul Island), 2: ***S. kalumburuana*** n. sp. (Kalumburu Mission), 3: ***S. herculea*** n. sp. (Eclipse Hill Island), 4: ***S. ngurraali*** n. sp. (Middle Osborn Island), 5: ***S. umbadayi*** n. sp. (Southwest Osborn Island), 6: ***S. wuyurru*** n. sp. (Bigge Island), 7: ***S. capillacea*** n. sp. (Boongaree Island), 8: ***S. garlinju*** n. sp. (Coronation Island), 9: ***S. gumalamala*** n. sp. (St Andrews Island), 10: ***S. insolita*** n. sp. (St Patrick Island), 11: *Setobaudinia* sp. (Augustus Island), 12: ***S. quinta*** n. sp. (Storr Island), 13: ***S. joycei*** n. sp. (Wulalam Island), 14: ***S. karczewski*** n. sp. (Molema Island); triangles = records of Solem (1985, 1991): 15: *S. pagoana* Solem, 1985 (near Kalumburu), 16: *S. calvitia* Solem, 1985 and *S. hirsuta* Solem, 1985 (Mitchell Plateau), 17: *S. doongana* Solem, 1985 (Carson River Escarpment), 18: *S. collingii* (Smith, 1893) (Parry Island), 19: *S. interrex* Solem, 1985 (Prince Regent Reserve); diamonds = records of undescribed taxa listed by Solem (1991): 20: *Setobaudinia* NSP6 (near Cape Bernier), 21: *Setobaudinia* NSP5 (Doubtful and Collier Bay area; probably at least partly identical with ***S. quinta***).

protoconch with well-developed microsculpture of regularly arranged, rather strongly developed tubercles; teleococonch lacking ribs, usually with very indistinct radial growth lines only, microsculpture of well-developed pustulation that form a regular pattern of parallel radial rows, frequently these projections support short periostracal setae or projections, often lost in adults, pustulation continuing on inner umbilical whorls; body whorl slightly to moderately descending, periphery well rounded. Shell colour uniform, yellowish brown to brown. Lip of aperture expanded, basal and palatal edges may be curved, outer palatal and basal nodes weak or absent, parietal wall inconspicuous.

Genital anatomy and *head wart*: Head with eversible head wart opening between and just posterior to ommatophores. Penis well developed, thick penial sheath extending entire length from insertion of retractor muscle to just above atrium; epiphallus well developed, tightly connected to penis by connective tissue, usually with well-developed epiphallic flagellum and epiphallic lobe. Inner penial wall completely covered with dense pustulation, pustules may be conspicuously laterally elongated or replaced by transverse pilasters or lateral lamellae, particularly at distal portion of penial wall, towards the proximal end, pustules often taper in size and shape. Most proximal part of penial wall usually weak; may become entirely dissolved resulting in detachment of the penis from the atrium (see Fig. 149, for instance). Penial retractor muscle attached at epiphallus near connection with penial complex. Epiphallus opens to penial lumen through large, conical verge with gutter forming along its tip. Inner epiphallic wall covered by characteristic armature of longitudinal ridges or pilasters and/or pustulation; vas deferens opens into epiphallus through slit-like, valvular opening. Free oviduct short, bent into S-shape. Bursa copulatrix elongated, tubular, extending to anterior end of albumen gland.

Aestivation Strategy

Free sealer (modified after Solem, 1985a).

Comparative Remarks

Species of *Setobaudinia* are readily distinguished from all other Kimberley camaenids except *Baudinella* by their usually small size, discoid shell, wide umbilicus, and typical pattern of microscopic periostracal projections; see above for comparison with *Baudinella*. Species subsumed under *Damochlora* are very similar in shell morphology and, where known, genital anatomy, differing essentially by larger size. However, some *Setobaudinia* species are exceptionally large, with shell diameter at magnitude of centimetres. Weakening or dissolution of posterior part of penial wall and partial or entire detachment of penis from atrium is a feature observed herein for the first time in any Australian camaenid. The functional significance of this detachment is unknown but believed to relate to a certain stage in reproductive development. Further typical combination of genital characteristics is presence of well-developed penial sheath, well-developed epiphallus with epiphallic flagellum and epiphallic lobe, large penial verge. These features are either not as well developed or absent in *Baudinella,* ***Molema*** and *Torresitrachia.* Shells of some species of *Torresitrachia* can be similar. Most conspicuously, they differ by a distinct microsculpture of the protoconch. The teleoconch of *Setobaudinia* differs by absence of well-developed axial ribs (usually present in the latter) and presence of periostracal pustulation or even hairs (usually absent in *Torresitrachia*). However, development of these microscopic features may vary considerably within both groups and may be difficult to detect in adult shells with worn periostracum.

Diversity and Distribution (Fig. 122)

Setobaudinia species are found along almost the entire Kimberley coast from Kalumburu in the north to near Derby in the south, including many islands. They are confined to rainforest patches and vine thickets. Solem (1985a, 1991) listed nine species, including undescribed taxa. In addition, 12 species are described herein from various islands of the Bonaparte and Buccaneer archipelagos between the Eclipse Archipelago in the north and Molema and Wulalam islands in the south. An additional species is transferred to *Setobaudinia* from *Damochlora*; one supposedly undescribed species from southern section of Augustus Island is known from a dry shell, which does not permit formal description (WAM S37274).

Setobaudinia rectilabrum
(E. A. Smith, 1894) n. comb
Figs. 123A, 124–126

Helix (*Cloritis*) *rectilabrum* E. A. Smith, 1894: 88, pl. VII, fig. 11.

Damochlora rectilabrum – Iredale, 1938: 98 (not Solem, 1979: 111–113; 1991: 185; Solem & McKenzie, 1991: 247–263).

Type Locality

Parry Harbour, northwestern Australia (Bougainville Peninsula).

Type Material

Lectotype BMNH 92.1.29.19 (shell); paralectotypes BMNH 92.1.29.20–1 (2 shells) (not examined).

Material Examined

WAM S49360 (2 preserved specimens), AM C471822 (5 shells), WAM S49345 (8 shells) from Bougainville Peninsula, Vansittart Bay, 13°55'58"S, 126°08'53"E; WAM S49339 (preserved specimen), WAM S49365 (6 preserved specimens), WAM S49361 (11 preserved specimens), AM C471826 (5 preserved specimens), AM C471823 (12 shells), AM C471824 (6 shells), AM C471825 (9 shells), WAM S49339 (12 shells), WAM S49340 (30 shells), WAM S49341 (18 shells), WAM S49342 (6 shells), WAM S49343 (2 shells), WAM S49344 (18 shells) from Wargul Wargul Island, Vansittart Bay, about 1.5 km W of Bougainville Peninsula.

Taxonomic Remarks

This species was described based on dry shell material from Parry Harbour, northwestern part of Bougainville Peninsula (~ 14°00'S, 126°00'E).

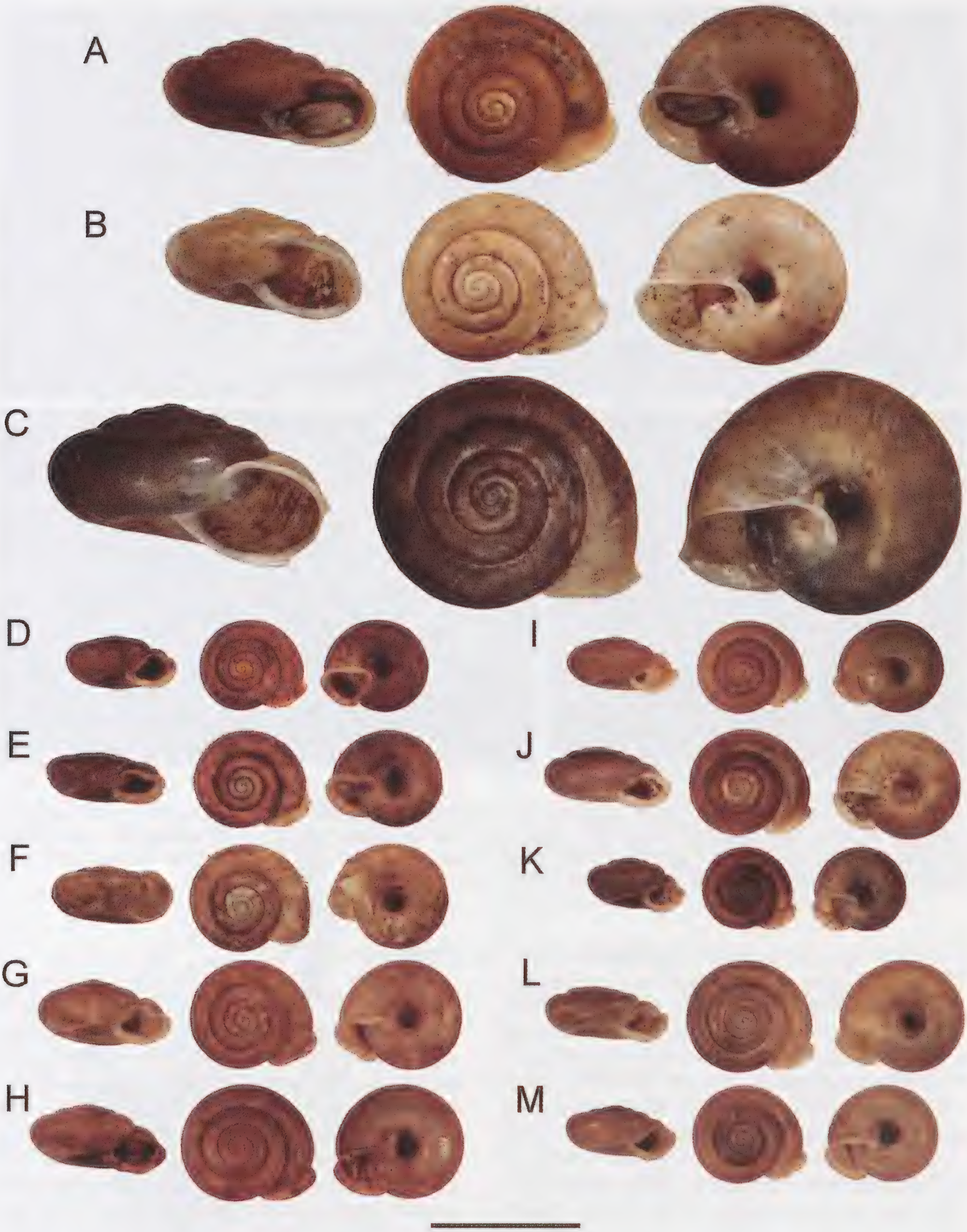

FIG. 123. Shells of *Setobaudinia*. A: *Setobaudinia rectilabrum* WAM S49361 (Wargul Wargul Island); B: ***Setobaudinia kalumburuana*** n. sp. paratype AM C106527 (Kalumburu); C: ***Setobaudinia herculea*** n. sp. paratype WAM S49346 (Eclipse Hill Island); D: ***Setobaudinia ngurraali*** n. sp. paratype WAM S36370 (Middle Osborn Island); E: ***Setobaudinia umbadayi*** n. sp. paratype WAM S36380 (Southwest Osborn Island); F: ***Setobaudinia wuyurru*** n. sp. paratype WAM S36352 (Bigge Island); G: ***Setobaudinia capillacea*** n. sp. paratype WAM S36361 (Boongaree Island); H: ***Setobaudinia garlinju*** n. sp. paratype WAM S33367 (Coronation Island); I: ***Setobaudinia gumalamala*** n. sp. paratype WAM S37268 (St Andrew Island); J: ***Setobaudinia insolita*** n. sp. paratype WAM S49044 (St Patrick Island); K: ***Setobaudinia quinta*** n. sp. paratype WAM S37889 (Storr Island); L: ***Setobaudinia joycei*** n. sp. paratype WAM S37885 (Wulalam Island); M: ***Setobaudinia karczewski*** n. sp. paratype WAM S37887 (Molema Island). Scale bar = 10 mm.

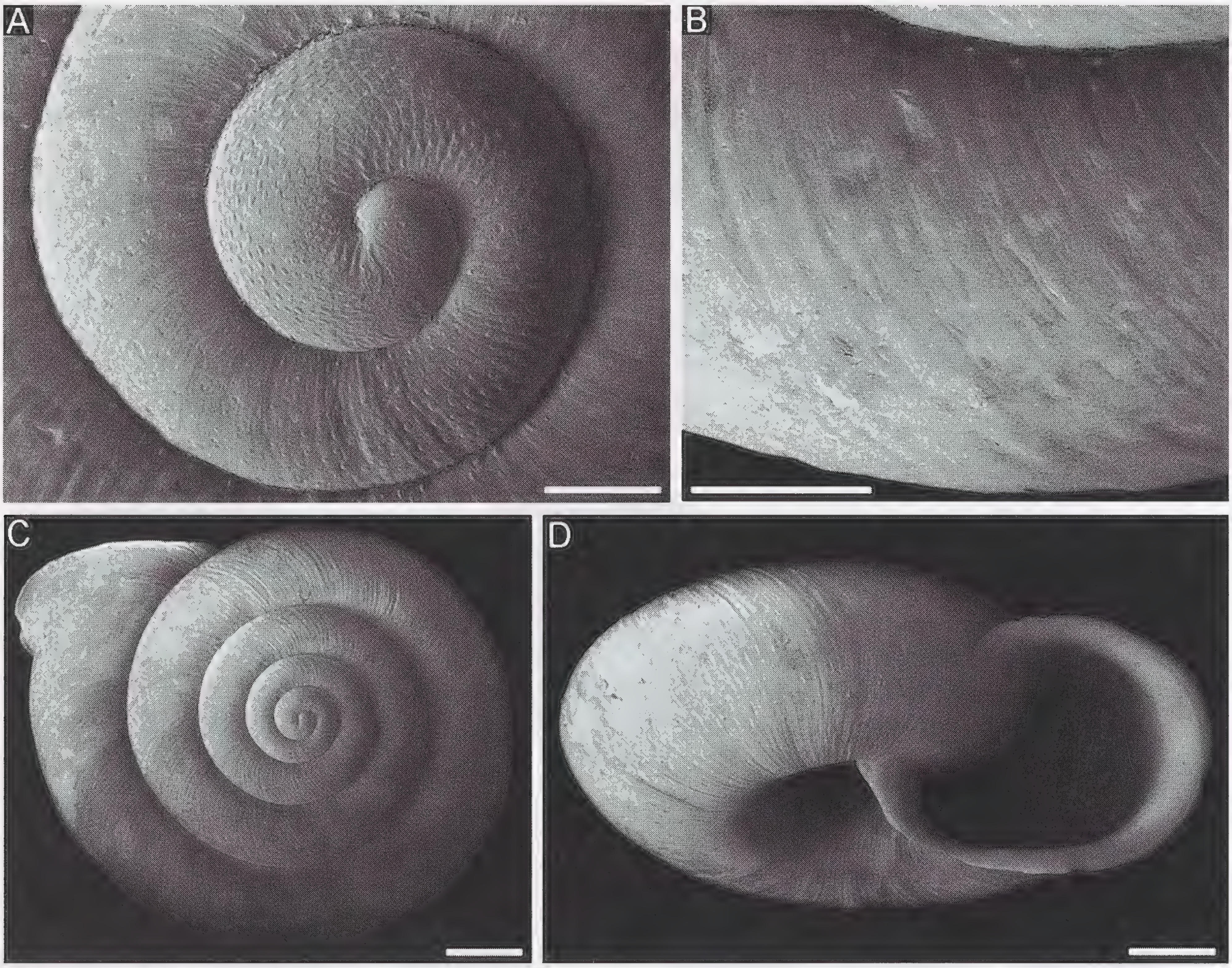

FIG. 124. SEM micrographs of the shell of *Setobaudinia rectilabrum* AM C471824 (Wargul Wargul Island). A: Apical view showing protoconch and first whorl. Scale bar = 500 µm; B: Close-up of sculpture on last whorl. Scale bar = 1 mm; C: Entire shell viewed from above; D: Entire shell viewed obliquely from below showing aperture. Scale bars C–D = 1 mm.

The lectotype has been designated by Solem (1979). Affiliated with *Damochlora* by Iredale, 1938, which was followed by Solem (1979, 1991), who published anatomical description based on examination of material from south of Kalumburu, Kimberley mainland (~ 14°18'S, 126°39'E), about 70 km SE from type locality. Material studied here from Bougainville Peninsula (~ 13°56'S, 126°08'E), immediately south of the type locality, revealed morphological features distinct from those described by Solem (1979: fig. 22). Based on this material, anatomy of the present species is redescribed. By contrast, Solem's (1979: 111–113) description of material from Kalumburu refers to an undescribed species, which is named below. *Helix rectilabrum* is transferred to *Setobaudinia* for showing features typical for this taxon. Treatment corroborated by mitochondrial phylogeny, in which all *Setobaudinia* species form a clade (Köhler, unpubl. data).

Description

Shell (Figs. 123A, 124): Large compared to most other congeners (D = 12.4 mm on average; Table 9), with low to weakly elevated spire; periphery well rounded to slightly angulated; umbilicus ~ 2 mm wide; colour light brownish-horn. Protoconch ~ 1.7 mm in diameter, comprising about one whorl, with dense radially arranged pustulation. Teleoconch with faint, regular radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal extensions; close-up images reveal traces of sparsely distributed, radially arranged periostracal pustules or extensions, which are worn off in adult shells. Last whorl not or weakly descending behind aperture; angle of aperture ~ 60°; apertural lip sharp, well expanded, slightly reflected, slightly flattened at base, without nodes, parietal wall delicate.

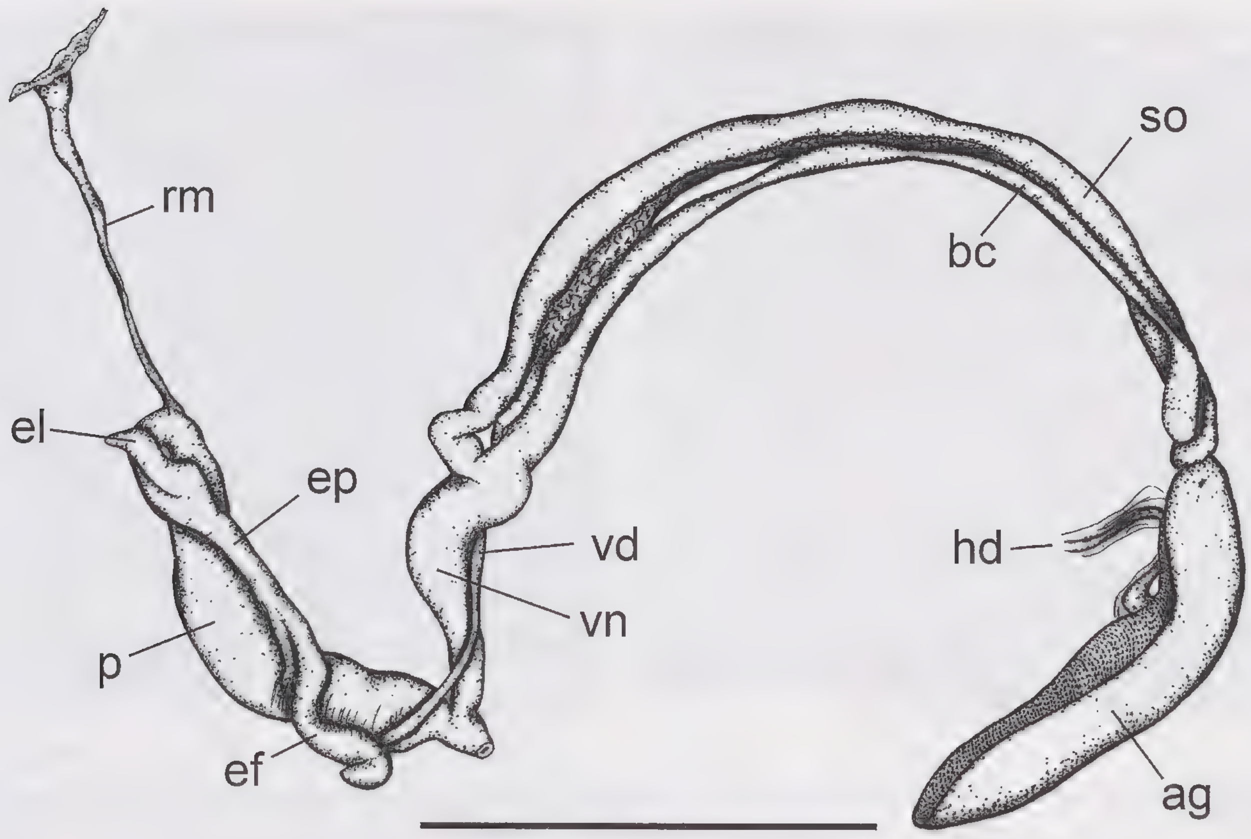

FIG. 125. Genital anatomy *Setobaudinia rectilabrum* AM C471826 (Wargul Wargul Island, June). Scale bar = 5 mm.

Genital anatomy (Figs. 125–126): Penis longer than vagina, rather straight. Epiphallus elongate, bent, more or less same length as penis, tightly connected to penis by connective tissue, with moderately long epiphallic flagellum, well-developed epiphallic lobe at opposite end. Interior penial wall completely covered with dense pustulation, pustules densely arranged in honeycomb pattern, large, triangular in shape, elevated; at distal portion pustules are laterally extended, longitudinally compressed, more densely packed giving rise to lateral lamellae at very distal end of wall. In the dissected specimen, penis detached from atrium through dissolved penial wall; connected to atrium by proximally thick penial sheath only. Inner epiphallic wall covered with very fine, densely packed longitudinal ridges, some of which give rise to elongated pustules. Penial retractor muscle long. Vagina longer than free oviduct, tubular to posteriorly expanded.

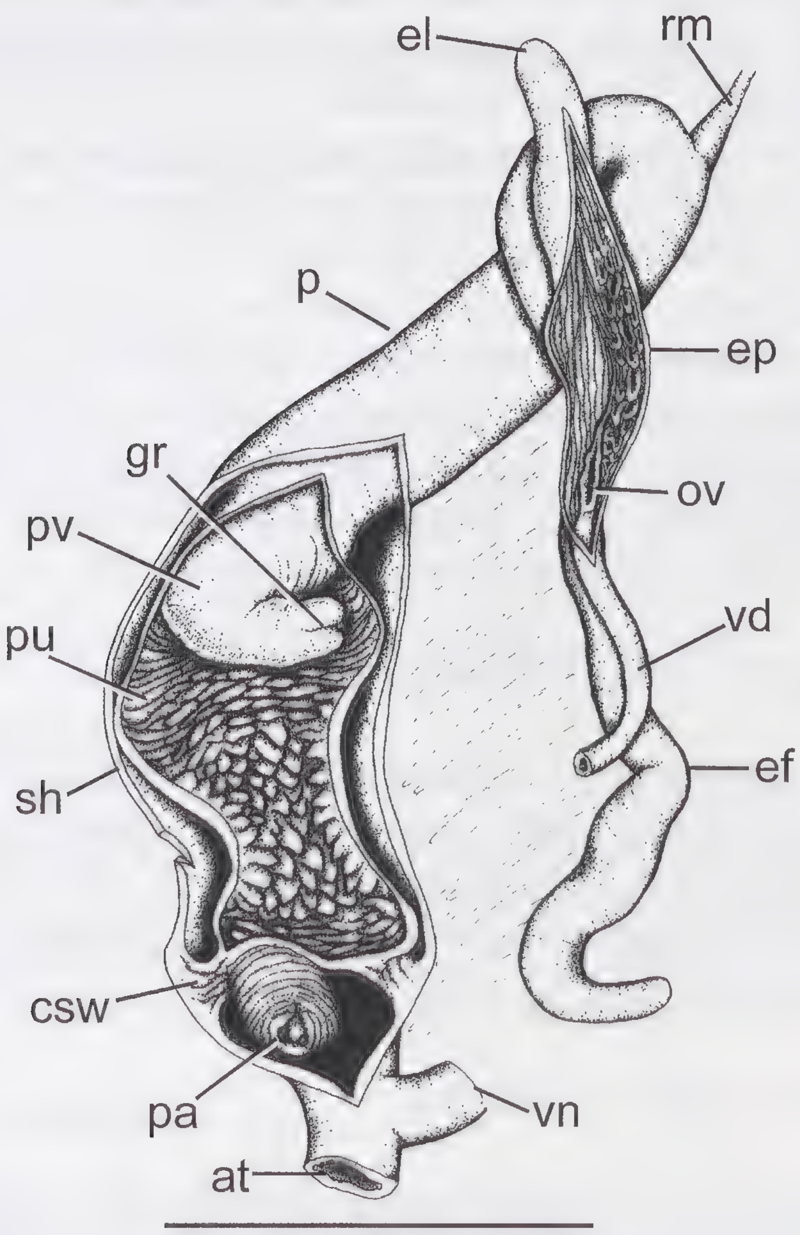

FIG. 126. Penial anatomy of *Setobaudinia rectilabrum* AM C471826 (Wargul Wargul Island, June). Scale bar = 2 mm.

Comparative Remarks

Shell similar to *Torresitrachia*, differing only by microscopic features of protoconch and teleoconch sculpture. Differs from most congeneric species by large size and rather smooth shell sculpture (but see below). Corresponding detachment of penis depicted by Solem (1979) for "*Damochlora rectilabrum*" = ***Setobaudinia kalumburana***; also found in ***S. insolita*** from St. Patrick Island (see below). Penial detachment has only been observed in three species of *Setobaudinia* is considered typical characteristic of the genus. Not observed in all species of the genus; may relate to a certain reproductive stage of individuals.

Distribution (Fig. 122)

Northern portion of Bougainville Peninsula.

Setobaudinia kalumburuana n. sp.
Fig. 123B

Damochlora rectilabrum – Solem, 1979: 111–113; 1991: 185; Solem & McKenzie, 1991: 247–263 (not *Helix* (*Cloritis*) *rectilabrum* E. A. Smith, 1894).

Type Locality

Western Australia, northwestern Kimberley, cliffs east of Kalumburu Mission, 14°18'S, 126°41'E; coll. P. Coleman, 12/06/1986 (dense rock scree on sandstone cliffs).

Material Examined

Holotype AM C150786 (preserved specimen). Paratypes AM C150786 (11 preserved specimens) from type locality; WAM 621.77 (preserved specimen, dissection by Solem, 1979) from NW-facing cave, 6.5 km S of Kalumburu Mission; AM C106527 (shell; Fig. 123A) from near Kalumburu Mission.

Additional, non-type material AM C133663 (shell), FMNH 199504, FMNH 199508, FMNH 200341, FMNH 200342, FMNH 200342, FMNH 200675, WAM S5103 (was WAM 359.77), WAM S5105 (was WAM 185.79) all from Kalumburu Mission area.

Etymology

For Kalumburu Reserve, adjective of feminine gender.

Taxonomic Remarks

Solem (1979) based anatomical description of "*Damochlora rectilabrum* E. A. Smith, 1894", on material collected near Kalumburu (WAM 621.77), which is evidently not conspecific with the species named by Smith (1894) from Parry Harbour and described above. Anatomical drawings depicted by Solem (1979: fig. 11; pl. 8a–c) reveal features different from *S. rectilabrum*. Material from around Kalumburu Mission is therefore considered to represent a distinct species, which herein is named ***Setobaudinia kalumburuana***. Like the genuine *S. rectilabrum* (E. A. Smith, 1894), this species is placed within *Setobaudinia* for revealing typical features of this genus. Because the specimen dissected by Solem (1979) could not be traced in collections of FMNH (Jochen Gerber, pers. comm.) and WAM (Corey Whisson, pers. comm.), here another specimen from Kalumburu is designated as holotype, which corresponds in anatomy with Solem's (1979) description. Molecular evidence from mitochondrial sequences of the AM type series corroborates distinct status of ***S. kalumburuana*** with respect to all other congeners.

Description

Shell (Fig. 123B): Large compared to other *Setobaudinia* species (D = 12.3 mm on average; Solem, 1979: 112), with low to weakly elevated spire; periphery well rounded to slightly angulated; umbilicus ~ 2 mm wide; colour light brownish-horn. Protoconch comprising about one whorl, with dense, radially arranged pustulation (Solem, 1979: pl. 8a–c). Teleoconch with faint, regular radial growth lines extending onto base of shell, replaced by microscopic hairs within umbilicus; microsculpture of short, radially arranged periostracal pustules and tiny ridglets, may be worn in adult shells. Last whorl not or weakly descending behind aperture; angle of aperture ~ 60°; apertural lip sharp, well expanded, slightly reflected, slightly flattened at base, without nodes, parietal wall delicate (adapted from Solem, 1979: 111–113).

Genital anatomy (illustrated by Solem, 1979: 102, fig. 22): Penis very long, coiled. Epiphallus moderate in size, bent, shorter than penis, with long epiphallic flagellum and well-developed epiphallic lobe at opposite end. Interior penial wall with dense rectangular pustules arranged in vertical rows, pustules replaced by lateral lamellae at very distal end of wall. Inner epiphallic wall covered with very fine, densely packed pustules arranged in longitudinal rows, anterior end near opening to penial lumen with fine longitudinal ridges. Penial retractor muscle moderately long. Vagina longer than free oviduct, tubular to posteriorly expanded.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.143–0.146 with respect to *S. rectilabrum* (2 sequences), 0.13 to ***S. herculea***, 0.147–0.185 to remaining congeners (31 sequences, 10 species).

Comparative Remarks

Shell not readily to be distinguished from *S. rectilabrum*; the latter stated by Solem (1979) to have an angulated periphery, which I cannot confirm as a general feature. Genital anatomy differs most conspicuously by arma-

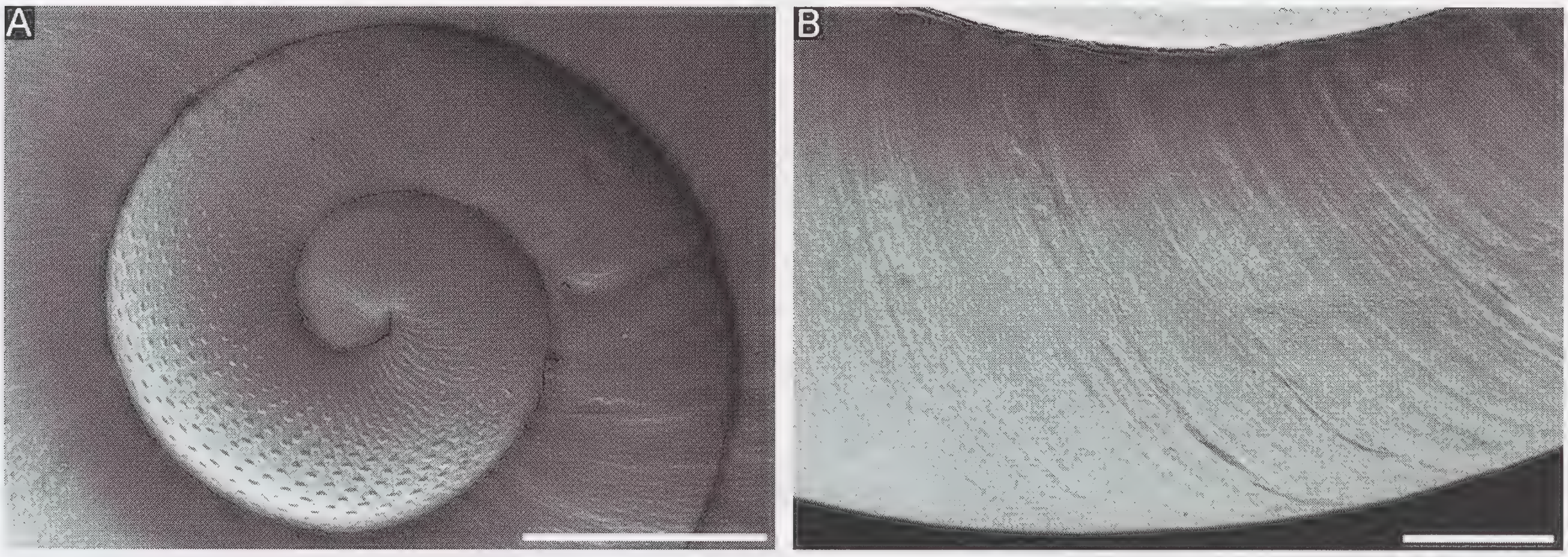

FIG. 127. SEM micrographs of the shell of ***Setobaudinia herculea*** n. sp. paratype AM C471827 (Eclipse Hill Island). A: Apical view showing protoconch and first whorl; B: Close-up of sculpture on last whorl. Scale bars = 1 mm.

ture of penial and epiphallic walls, penial wall pustules rectangular instead of triangular in *S. rectilabrum*; inner epiphallic wall with pustules instead of longitudinal ridges in *S. rectilabrum*. For comparison with ***S. herculea***, another species with similar shell see below. All other congeners differ most conspicuously by much smaller size of shell.

Distribution (Fig. 122)

Mainland, around Kalumburu Mission.

Setobaudinia herculea n. sp.
Figs. 123C, 127, 128

Type Locality

Western Australia, northern Kimberley, Vansittart Bay, Eclipse Archipelago, Eclipse Hill Island, 13°56’31”S, 126°17’01”E; coll. Vince Kessner, 04/06/2010, KIS 3–198 (vine thicket on upper slopes, laterite; under rocks).

Material Examined

Holotype WAM S58470 (preserved specimen). Paratypes WAM S49353 (5 preserved specimens), AM C471827 (3 shells), WAM S49346 (6 shells) from type locality.

Etymology

Derived from “*herculeus*” (Latin = herculean), in reference to its unusually large size; adjective of feminine gender.

Description

Shell (Figs. 123C, 127): Very large compared to other congeners (D = 18.9 mm on average; Table 9) with weakly elevated spire; well-rounded to slightly angulated periphery; umbilicus on average 3.5 mm wide; colour light brownish-horn. Protoconch ~ 2.2 mm in diameter, comprising ~ 1.2 whorls, with regular, radially arranged pustulation. Teleoconch with faint, regular radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal extensions; close-up images reveal traces of sparsely distributed, radially arranged periostracal pustules or extensions; worn in adult shells. Last whorl not or weakly descending behind aperture; angle of aperture ~ 60°; aperture wide, with sharp, flaring, slightly reflected lip, flattened at base, without nodes or only trace of basal node, parietal wall delicate.

Genital anatomy (Fig. 128): Penis longer than vagina, rather straight. Epiphallus elongate, bent, more or less same length as penis, tightly connected to penis by connective tissue, with very long epiphallic flagellum and well-developed epiphallic lobe. Interior penial wall completely covered with dense pustulation, pustules arranged in longitudinal rows, large, triangular in shape, elevated; no traces of transverse lamellae at distal end. Inner epiphallic wall covered with well-developed longitudinal pilasters, replaced by crowded, irregularly shaped pustules within epiphallic lobe. Penial retractor muscle long. Vagina longer than free oviduct, tubular to posteriorly expanded.

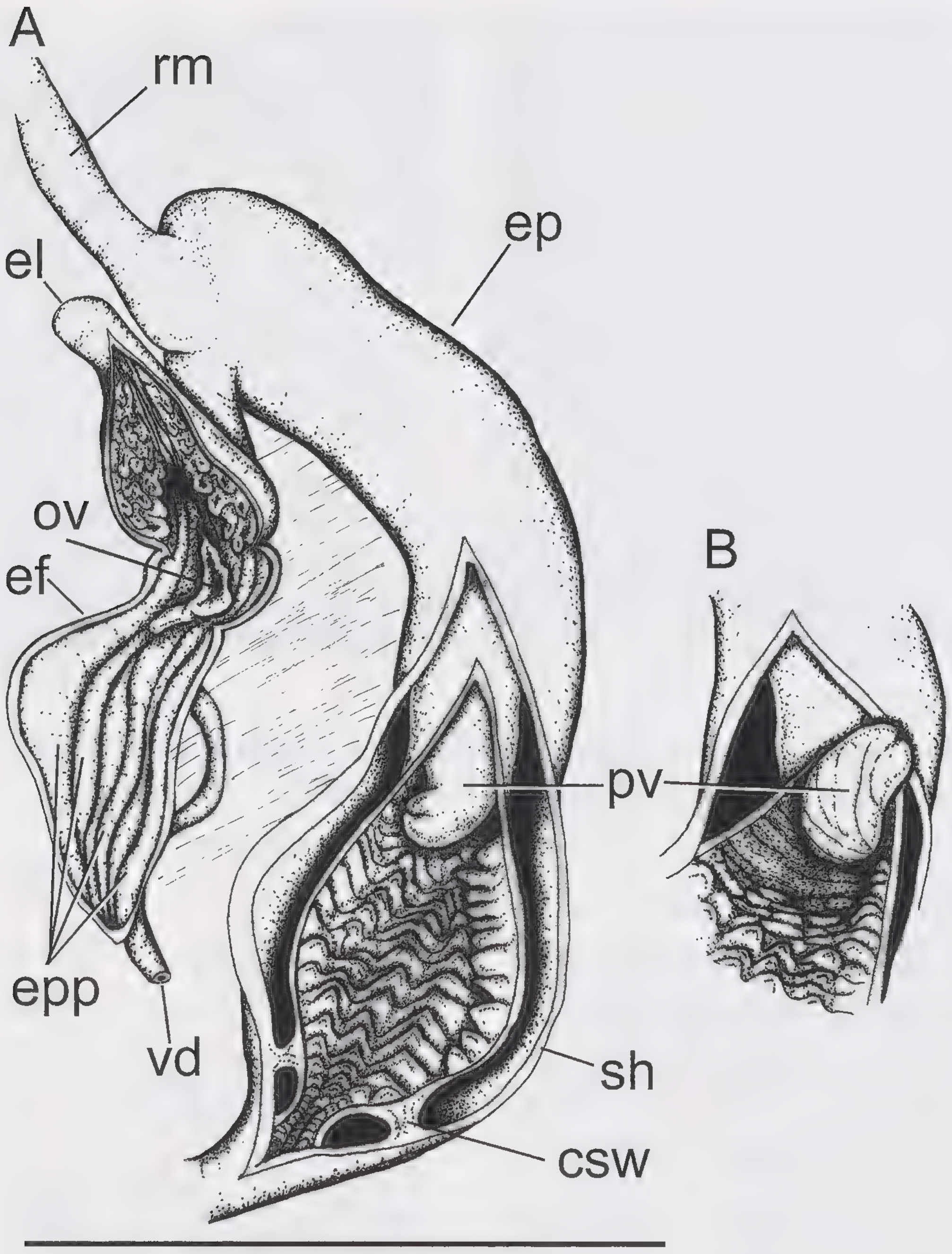

FIG. 128. Penial anatomy of ***Setobaudinia herculea*** n. sp. paratype WAM S49353 (Eclipse Hill Island, June). Scale bar = 4 mm.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.07–0.071 with respect to *S. rectilabrum* (2 sequences), 0.13 to ***S. kalumburuana***, 0.147–0.185 to remaining congeners (31 sequences, 10 species).

Comparative Remarks

For comparison with *Torresitrachia,* see general remarks under genus. Shell similar to *S. rectilabrum* and ***S. kalumburuana*** but considerably larger, with wider aperture and more strongly expanded lip. Characteristic features of genital anatomy are penial wall with triangular pustules arranged in longitudinal rows (honeycomb pattern in *S. rectilabrum*), no transverse lamellae or ridges (like in *S. rectilabrum* and ***S. kalumburuana***), penial verge proportionally smaller than in former two species. Proximal end of penis not found to be detached from atrium wall but corresponding portion being narrow and thin indicating similarities with above described features.

Distribution (Fig. 122)

Eclipse Hill Island, Eclipse Archipelago.

Setobaudinia ngurraali n. sp.
Figs. 123D, 129–131

Type Locality

Western Australia, NW Kimberley, Bonaparte Archipelago, Admiralty Gulf, Middle Osborn Island, 14°18’43”S, 126°01’41”E; coll. Vince Kessner, 9/02/2008, KIS 2–28 (vine thicket adjacent to a creek with boulders; in leaf litter).

Material Examined

Holotype WAM S58471 (preserved specimen). Paratypes WAM S36898 (preserved specimen), WAM S36945 (10 shells), WAM S36944 (70 shells), AM C471828 (30 shells), WAM S36366 (8 shells), WAM S58472 (2 preserved specimens), WAM S36714 (9 preserved specimens), WAM S36367 (3 shells), WAMS 36368 (3 shells), WAM S36369 (6 shells), WAM

S36370 (23 shells) from east coast of Middle Osborn Island.

Additional, non-type material. WAM S36371 (6 shells), WAM S36385 (7 shells), WAM S36714 (9 preserved specimens), WAM S36715 (2 preserved specimens), WAM S36716 (preserved specimen), WAM S36717 (6 preserved specimens), WAM S36718 (5 preserved specimens), WAM S36899 (preserved specimen), WAM S58473 (6 preserved specimens) from east coast of Middle Osborn Island.

Etymology

For Ngurraali, name of Middle Osborn Island in Gaambera, language of the Uunguu people; noun in apposition.

Description

Shell (Figs. 123D, 129): Small (D = 7.2 mm on average; Table 9), with low to weakly elevated spire; last whorl slightly angulated above periph-

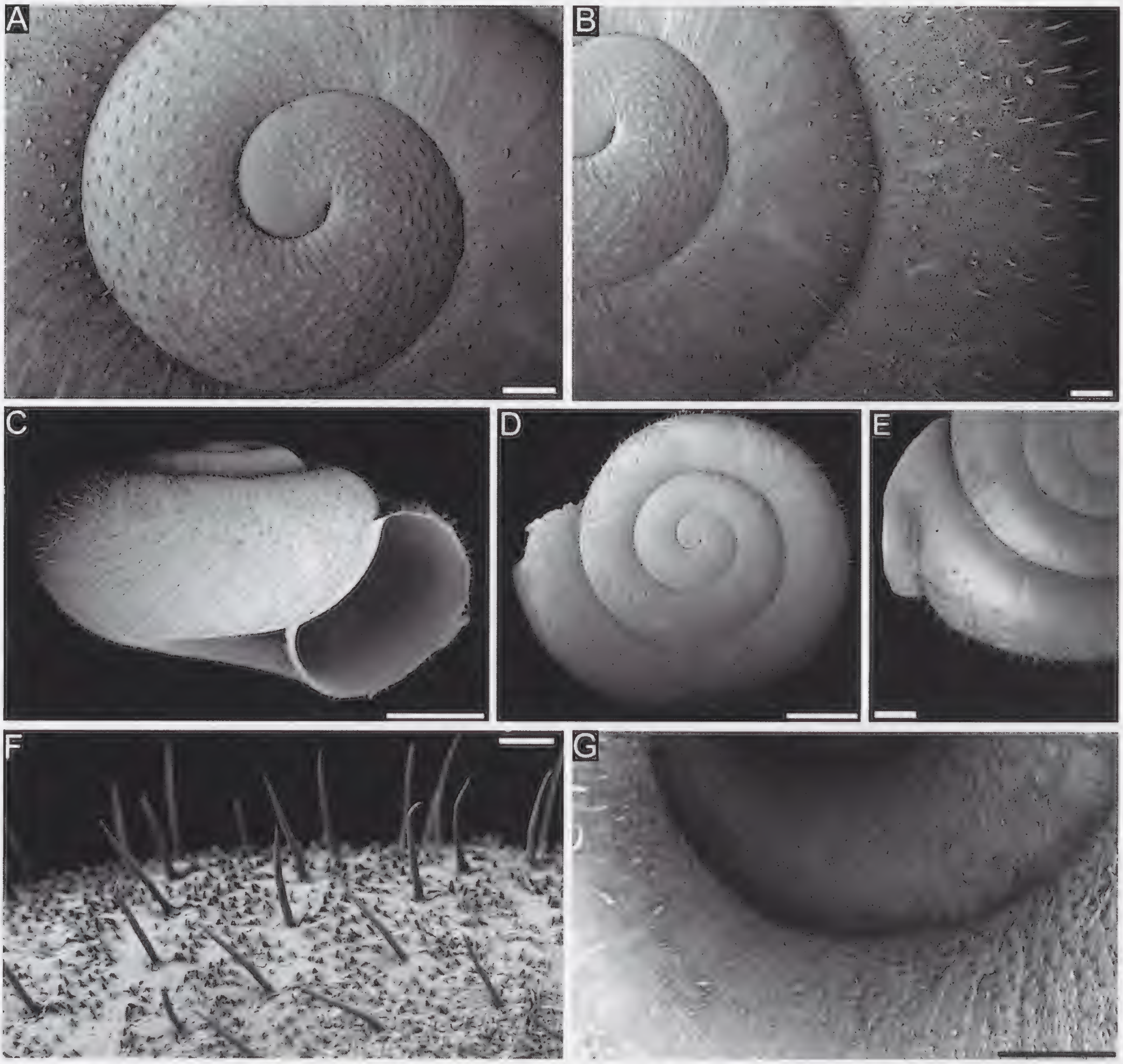

FIG. 129. SEM micrographs of the shell of ***Setobaudinia ngurraali*** n. sp. paratype AM C471828 (Middle Osborn Island). A: Apical view showing protoconch; B: Sculpture across first three whorls viewed from above. Scale bars A–B = 200 μm; C: Sub-adult shell with periostracal hairs, lateral view; D: Sub-adult shell, viewed from above; E: Last whorl, kinked behind apertural lip. Scale bars C–E = 1 mm; F: Close-up of last whorl of sub-adult shell showing periostracal hairs and periostracal granules in higher magnification. Scale bar = 100 μm; G: Close-up of inner umbilicus showing periostracal granules. Scale bar = 200 μm.

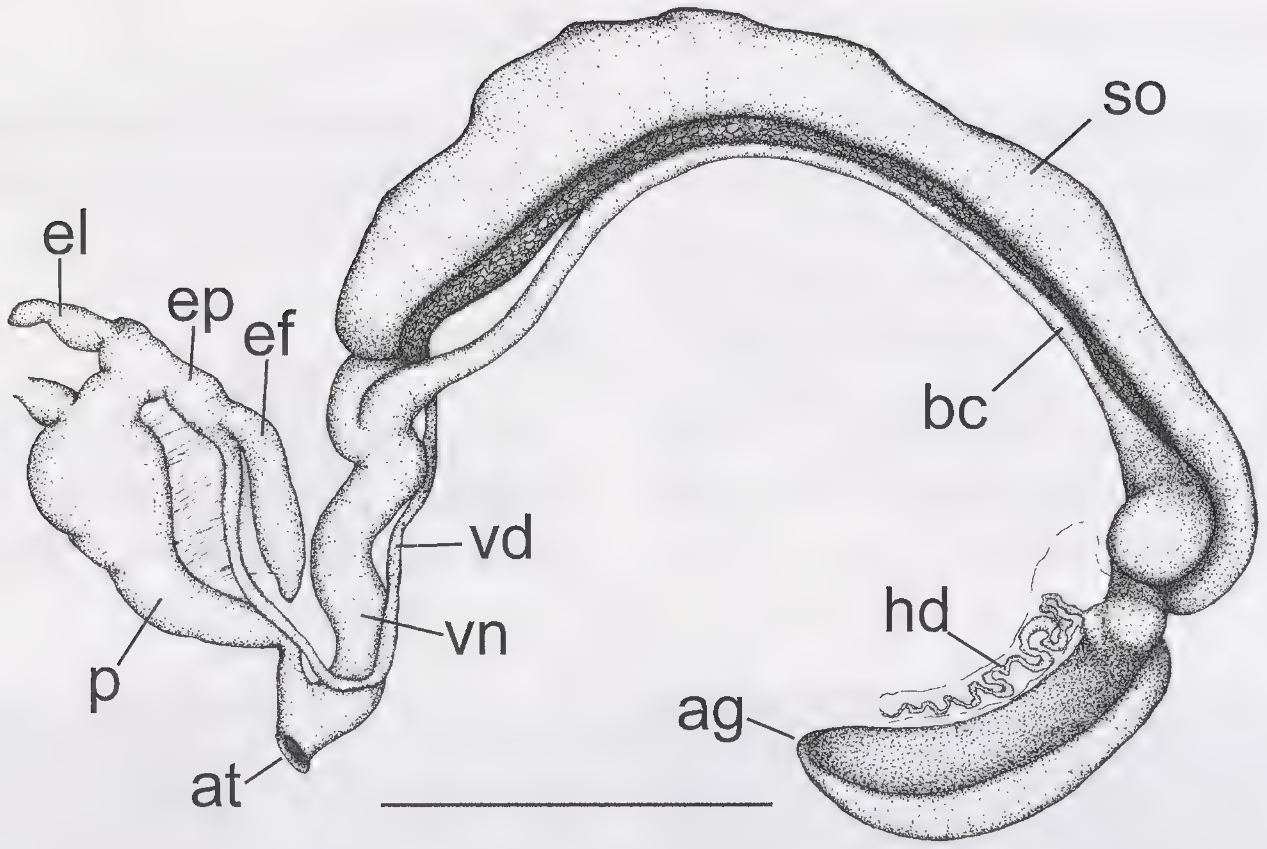

FIG. 130. Genital anatomy of ***Setobaudinia ngurraali*** n. sp. holotype WAM S49353 (Middle Osborn Island, February). Scale bar = 3 mm.

ery; umbilicus on average 1.9 mm wide; colour yellowish brownish. Protoconch ~ 1.5 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell densely covered with radially arranged periostracal hairs (usually worn off in adults) and microscopic granules. Last whorl shortly descending behind aperture, kinked immediately behind lip; angle of aperture ~ 60°; aperture wide, with sharp, well-expanded, reflected lip, flattened at base with well-developed basal node; palatal portion of lip intended, with weak palatal node, parietal wall delicate.

Genital anatomy (Figs. 130–131): Penis as long as vagina, straight. Epiphallus well developed, same length as penis, with very long epiphallic flagellum and well-developed epiphallic lobe. Interior penial wall completely covered with densely packed, transverse to oblique lamellar pilasters, partitioned by longitudinal gutters, gradually transforming into longitudinal lamellar pilasters towards proximal end of penial wall. Penial retractor muscle short. Vagina longer than free oviduct, tubular to posteriorly expanded.

Mitochondrial Differentiation

Infraspecific genetic distances (6 sequences): 0.0–0.024; interspecific genetic distances: 0.063–0.085 with respect to ***S. umbadayi*** (5 sequences), 0.147–0.182 to all remaining congeners (24 sequences, 11 species).

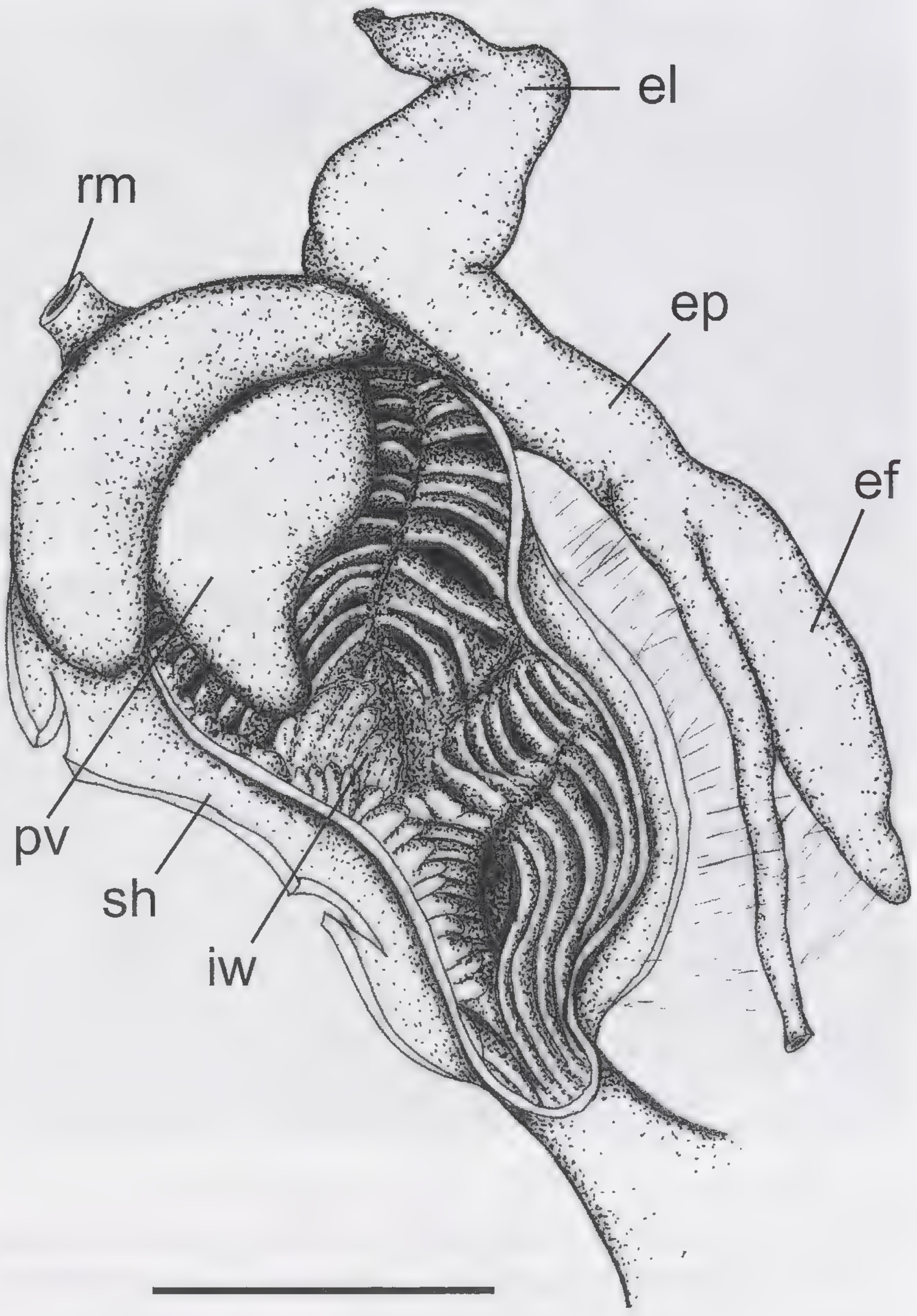

FIG. 131. Penial anatomy of ***Setobaudinia ngurraali*** n. sp. holotype WAM S58471 (Middle Osborn Island, February). Scale bar = 1 mm.

Comparative Remarks

Shell most similar to *S. hirsuta* Solem, 1985, with regard to features stated to be typical for this species (Solem, 1985a: 755–756), such as presence of pointed periostracal hairs, and indented parietal margin of apertural lip but differing conspicuously in inner penial wall anatomy (with irregularly arranged pilasters in *S. hirsuta*); similarly pilasters shifting from circular to longitudinal arrangement. The second species from mainland localities close to Middle Osborn Island, *S. calvitia* Solem, 1985, differs most conspicuously by pustulose armature of inner penial wall. *Setobaudinia collingii* has larger shells, lacks densely packed periostracal hairs. See below for comparison with ***S. umbadayi***.

Distribution (Fig. 122)

Middle Osborn Island, in western part of island in sympatry with ***S. umbadayi***, which appears to be more abundant there.

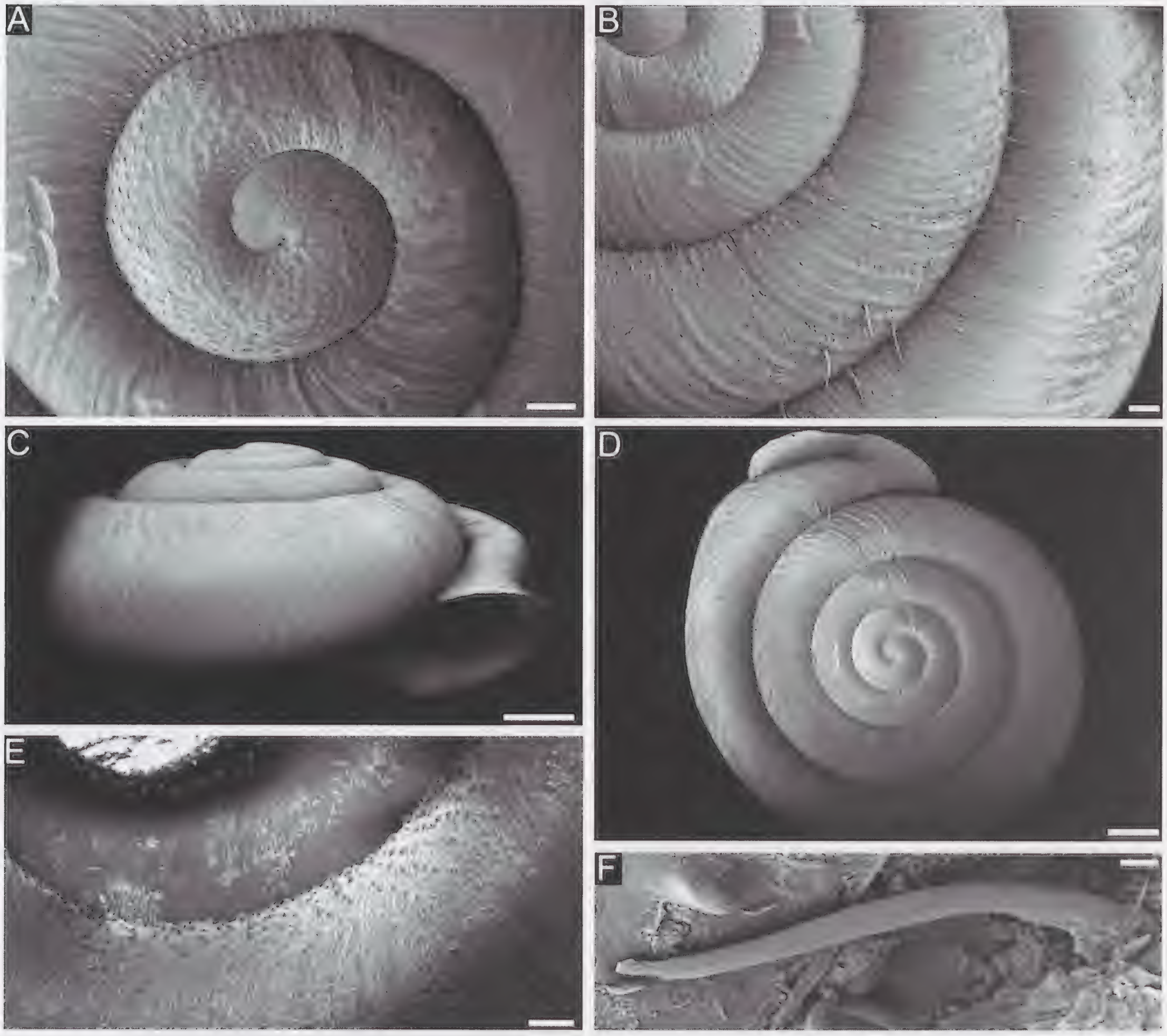

FIG. 132. SEM micrographs of the shell of ***Setobaudinia umbadayi*** n. sp. paratype AM C471830 (Southwest Osborn Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above. Scale bars A–B = 200 μm; C: Shell, lateral view; D: Shell viewed from above. Scale bars C–D = 1 mm; E: Close-up of inner umbilicus showing periostracal granules. Scale bar = 200 μm; F: Close-up of periostracal hair. Scale bar = 100 μm.

Setobaudinia umbadayi n. sp.
Figs. 123E, 132–134

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Admiralty Gulf, W coast of Southwest Osborn Island, 14°22'29"S, 125°56'19"E; coll. Vince Kessner, 30/07/2007, KIS 3–8 (vine thicket on steep, upper slopes near base of cliffs, volcanic scree and boulders; in leaf litter, under rocks).

Material Examined

Holotype WAM S58474 (preserved specimen, dissected). Paratypes WAM S36708 (19 preserved specimens), AM C471829 (6 preserved specimens), WAM S36709 (8 preserved specimens), WAM S36374 (25 shells), AM C471830 (16 shells), WAM S36379 (23 shells), WAM S36380 (22 shells) from west coast of Southwest Osborn Island.

Additional, non-type material. WAM S36375 – WAM S36378, WAM S36381 – WAM S36384, WAM S36948 – WAM S36950, AM C471831 (shells), WAM S36702 – WAM S36707, WAM S36710 – WAM S36712, WAM S36901, AM C471832 (preserved specimens) from west coast of Southwest Osborn Island; WAM S36719 – WAM S36721 (preserved specimens), WAM S36946 – WAM S36947, WAM S36372 – WAM S36373, AM C471833 (shells) from west coast of Middle Osborn Island.

Etymology

For Umbadayi, name of Southwest Osborn Island in Gaambera, language of the Uunguu people; noun in apposition.

Description

Shell (Figs. 123E, 132): Small (D = 7.4 mm on average; Table 9), with low to weakly elevated spire; last whorl slightly angulated above periphery; umbilicus on average 2.1 mm wide; colour yellowish brownish. Protoconch ~ 1.3 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell densely covered with radially arranged periostracal hairs (usually worn in adults) and microscopic granules. Last whorl shortly descending behind aperture, kinked immediately behind lip; angle of aperture ~ 60°; aperture wide, with sharp, strongly expanded and reflected lip, flattened at base with strongly developed basal node; palatal portion of lip intended, with weak palatal node, parietal wall delicate.

Genital anatomy (Figs. 133–134): Penis as long as vagina, straight. Epiphallus well devel-

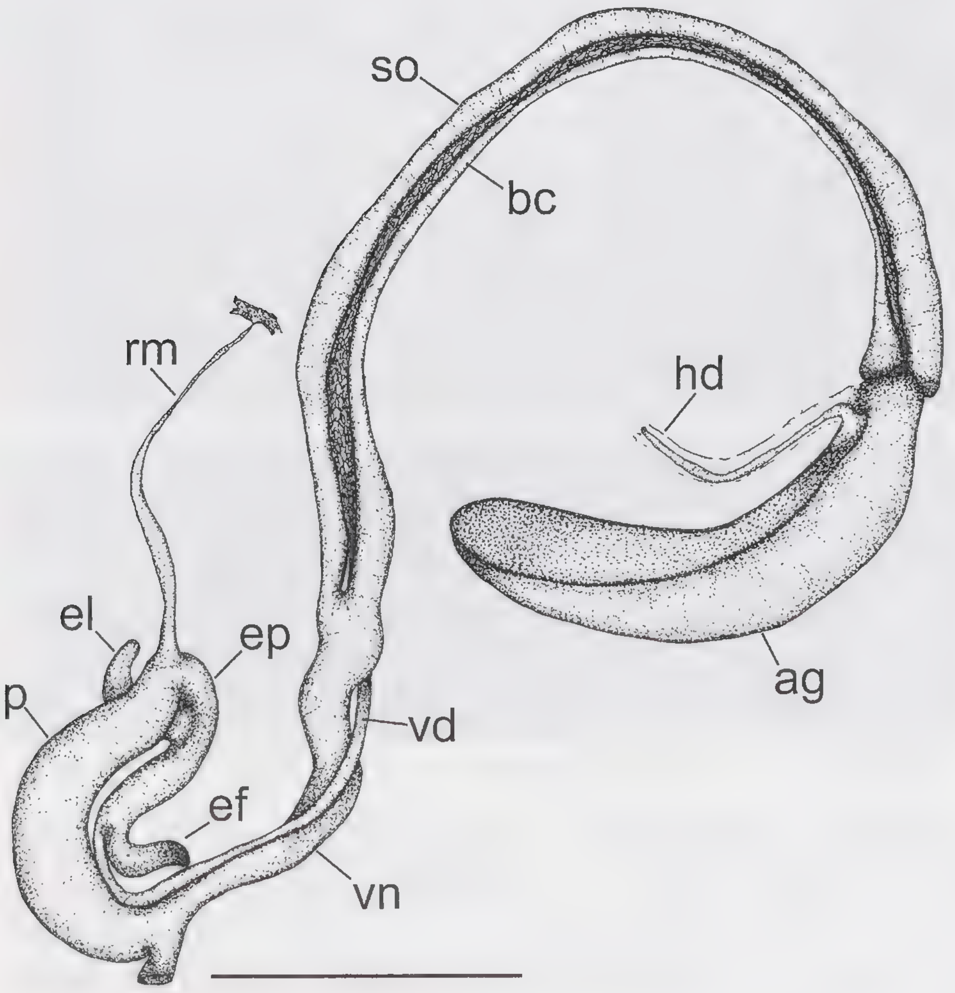

FIG. 133. Genital anatomy of ***Setobaudinia umbadayi*** n. sp. holotype WAM S58474 (Southwest Osborn Island, July). Scale bar = 2 mm.

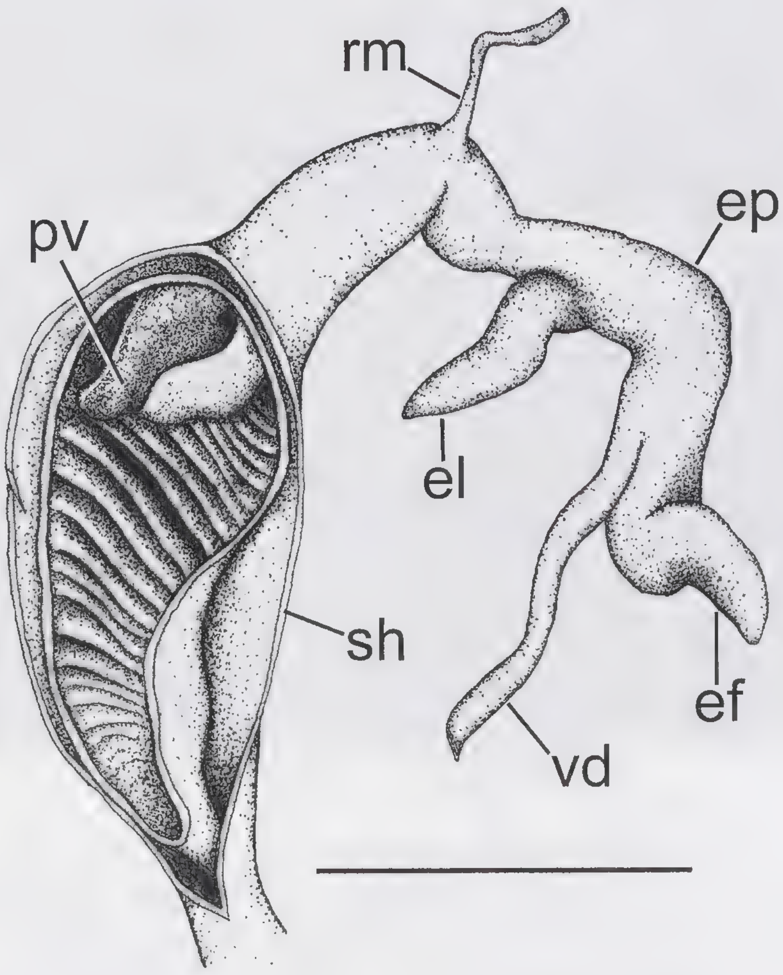

FIG. 134. Penial anatomy of ***Setobaudinia umbadayi*** n. sp. holotype WAM S58474 (Southwest Osborn Island, July). Scale bar = 1 mm.

oped, more or less as long as penis, with very long epiphallic flagellum and well-developed epiphallic lobe. Interior penial wall completely covered with densely packed, transverse to slightly oblique lamellar pilasters, their elevation tapering towards proximal end of penial wall. Penial retractor muscle short. Vagina longer than free oviduct, tubular to posteriorly expanded.

Mitochondrial Differentiation

Infraspecific genetic distances (5 sequences): 0.0–0.049; interspecific genetic distances: 0.063–0.085 with respect to ***S. ngurraali*** (6 sequences), 0.154–0.172 to all remaining congeners (24 sequences, 11 species).

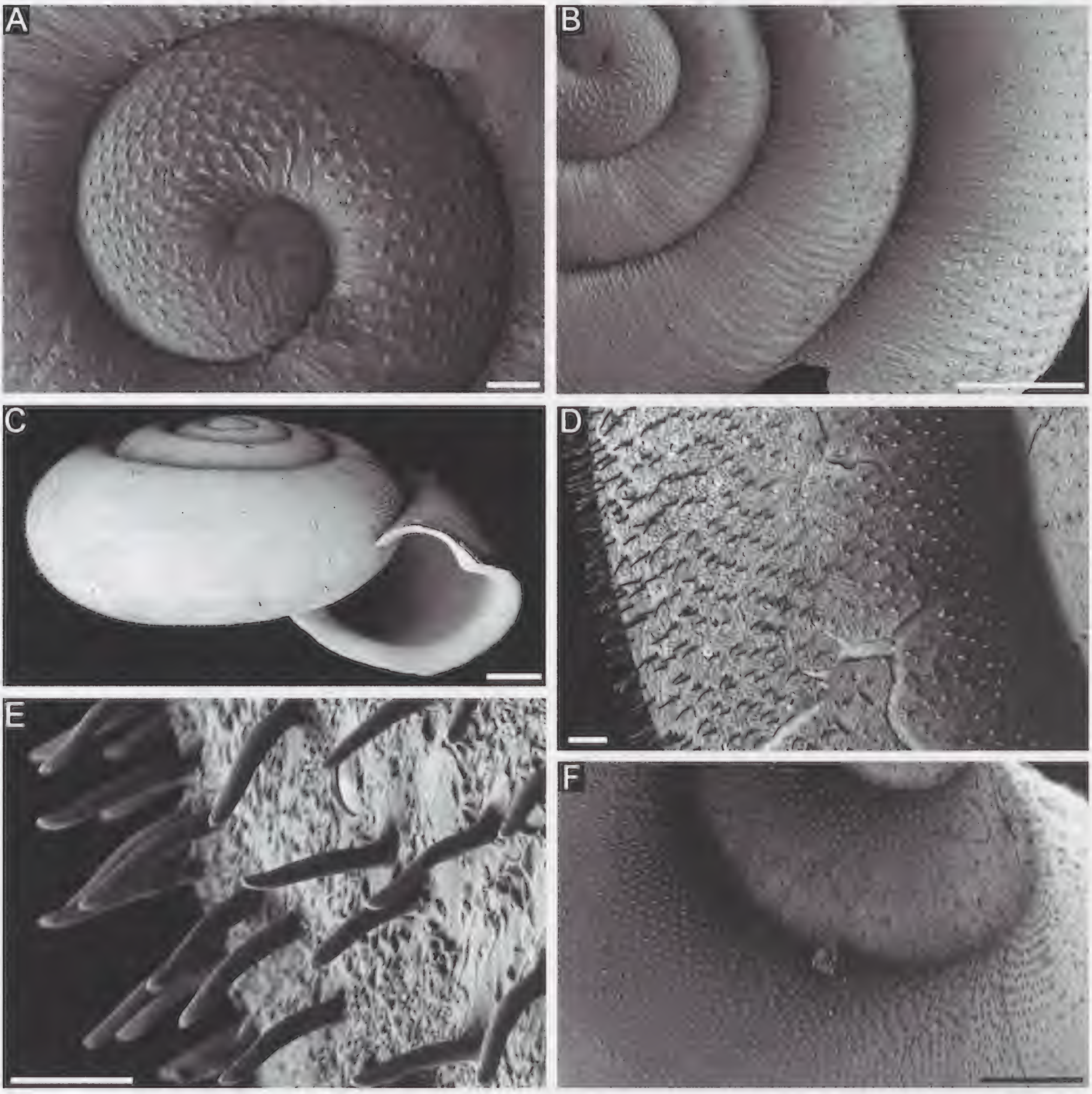

FIG. 135. SEM micrographs of the shell of ***Setobaudinia wuyurru*** n. sp. (Bigge Island). A–B: Paratype AM C471834. A: Apical view showing protoconch. Scale bar = 200 µm; B: Sculpture across entire shell viewed from above. Scale bar = 1 mm; C–F: Paratype WAM S36749. C: Shell, frontal view showing aperture. Scale bar = 1 mm; D: Last whorl viewed from obliquely from above showing periostracal hairs. Scale bar = 200 µm; E: Close-up showing periostracal hairs on last whorl. Scale bar = 100 µm; F: Close-up inner umbilical whorls showing periostracal granules. Scale bar = 500 µm.

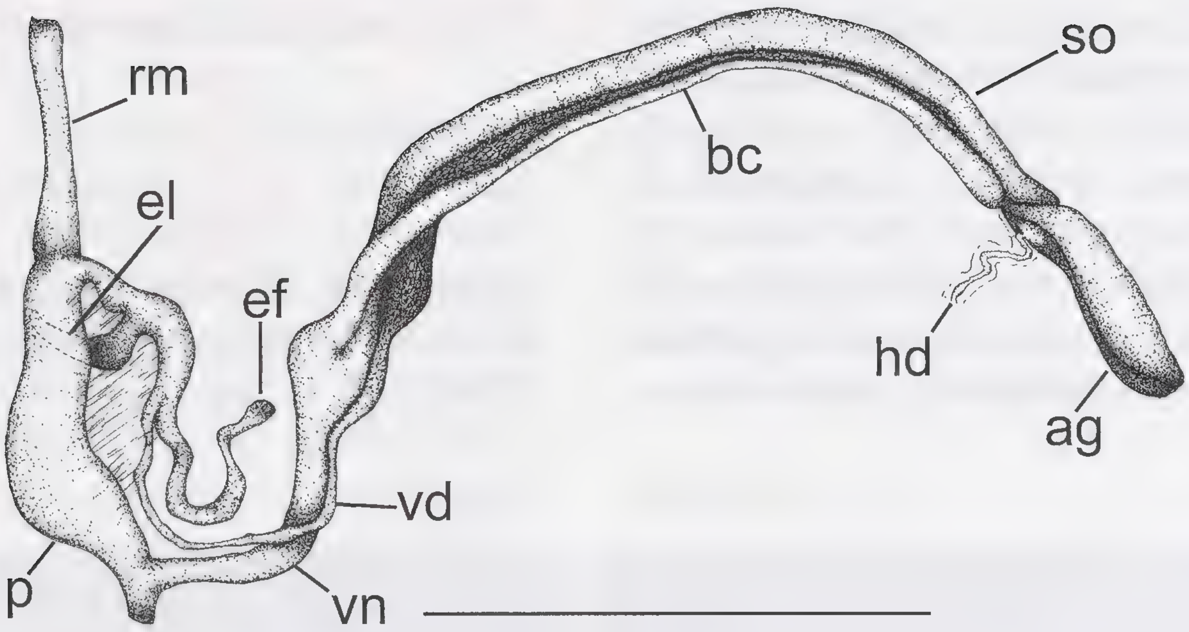

FIG. 136. Genital anatomy of ***Setobaudinia wuyurru*** n. sp. holotype WAM S58475 (Bigge Island, August). Note that the epiphallic lobe (el) is partly concealed. Scale bar = 3 mm.

Comparative Remarks

Most similar to its putative sister species ***S. ngurraali*** from Middle Osborn Island. The lot WAM 36719 from western coast of Middle Osborn Island was found to contain both specimens of ***S. ngurraali*** and ***S. umbadayi***, proving that both species occur in sympatry in parts of their ranges. Apertural lip more strongly expanded and reflected in ***S. umbadayi***; most conspicuous difference is simpler armature of inner penial wall and lack of longitudinal pilasters or gutters. For comparison with *S. hirsuta*, *S. calvitia* and *S. collingii* compare with ***S. ngurraali***.

Distribution (Fig. 122)

Southwest Osborn Island and western portion of Middle Osborn Island (here in sympatry with ***S. ngurraali***); occurrence on Kidney Island in between both islands likely.

Setobaudinia wuyurru n. sp.

Figs. 123F, 135–137

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, west coast of Bigge Island, 9.17 km NW of Savage Hill, 14°35'12"S, 125°06'13"E; coll. Michael Shea, 3/08/2007, KIS 1–18 (rocky ridge top with caves and vine thicket; in leaf litter between rocks).

Material Examined

Holotype WAM S58475 (preserved specimen). Paratypes WAM S36749 (2 preserved specimens), WAM S36974 (preserved specimen), WAM S36351 (3 shells), WAM S36352 (4 shells, Fig. 123F), AM C471834 (shell), WAM S58476 (3 preserved specimens), WAM S36353 (4 shells), WAM S36354 (shell), WAM S36355 (6 shells), AM C471835 (2 shells), WAM S36356 (8 shells), WAM S36748 (shell) from west coast of Bigge Island.

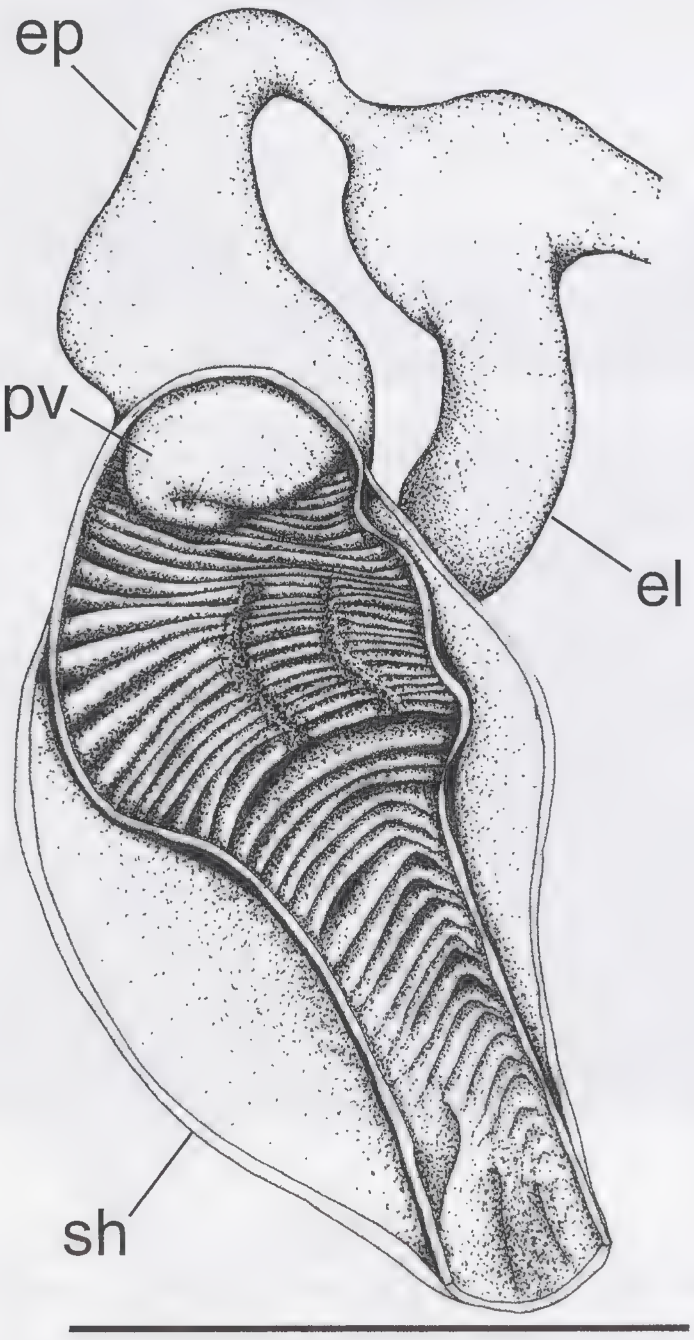

FIG. 137. Penial anatomy of ***Setobaudinia wuyurru*** n. sp. holotype WAM S58475 (Bigge Island, August). Scale bar = 1 mm.

Etymology

For Wuyurru, name of Bigge Island in Wunambal, language of the Uunguu people; noun in apposition.

Description

Shell (Figs. 123F, 135): Small (D = 8.5 mm on average; Table 9), with low to weakly elevated spire; periphery well rounded; umbilicus on average 2.5 mm wide; colour light yellowish brownish. Protoconch ~ 1.1 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell densely covered with radially arranged, short periostracal hairs (usually worn off in adults) and microscopic granules, which are pronounced underneath suture. Last whorl weakly descending behind aperture, slightly kinked immediately behind lip; angle of aperture ~ 60°; aperture wide, with sharp, weakly expanded and reflected lip, slightly flattened at base, basal node weak or absent; palatal portion of lip slightly intended, parietal wall delicate.

Genital anatomy (Figs. 136–137): Penis as long as vagina, straight. Epiphallus as long as penis, attached to penis by connective tissue, with very long epiphallic flagellum and well-developed epiphallic lobe. Interior penial wall completely covered with densely packed, transverse to slightly oblique lamellar pilasters, their elevation tapering towards proximal end of penial wall, in mid-portion divided by longitudinal gutters on posterior portion of wall. Penial retractor muscle short. Vagina longer than free oviduct, tubular to posteriorly expanded.

Mitochondrial Differentiation

Infraspecific genetic distances (2 sequences): 0.007; interspecific genetic distances: 0.154–0.182 to all remaining congeners (33 sequences, 12 species).

Comparative Remarks

Shell slightly larger than ***S. ngurraali*** and ***S. umbadayi***, with weaker indention, expansion and reflection of lip, shorter periostracal hairs. Inner penial wall most similar to ***S. ngurraali***, which lacks longitudinal gutters. Species genetically well differentiated.

Distribution (Fig. 122)

Bigge Island.

Setobaudinia capillacea n. sp.
Figs. 123G, 138–140

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04’22”S, 125°10’56”E; coll. Michael Shea, 7/08/2007, KIS 1–27 (dry open eucalypt woodland or grassland with baobab on dolerite; in soil under litter).

Material Examined

Holotype WAM S58477 (preserved specimen). Paratypes WAM S36752 (3 preserved specimens), WAM S36357 (14 shells), WAM S36358 (10 shells), AM C471836 (9 shells), WAM S36359 (30 shells), AM C471837 (10 shells), WAM S36360 (10 shells), WAM S36361 (6 shells), WAM S36362 (shell), WAM S36363 (2 shells), WAM S36364 (14 shells), WAM S36365 (4 shells), WAM S36750 (preserved specimen), WAM S36751 (4 preserved specimens), WAM S36753 (5 preserved specimens), AM C471838 (3 preserved specimens), WAM S36754 (2 preserved specimens), WAM S37688 (8 preserved specimens), WAM S36755 (7 preserved specimens) from central section of Boongaree Island.

Etymology

Derived from “*capillaceus*” (Latin, masculine = hairy), referring to dense coverage of shell with short periostracal hairs; adjective of feminine gender.

Description

Shell (Figs. 123G, 138): Small (D = 8.8 mm on average; Table 9), with weakly to moderately elevated spire; periphery well rounded; umbilicus on average 2.5 mm wide; colour light yellowish brownish. Protoconch ~ 1.2 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell densely covered with triangularly shaped periostracal extensions

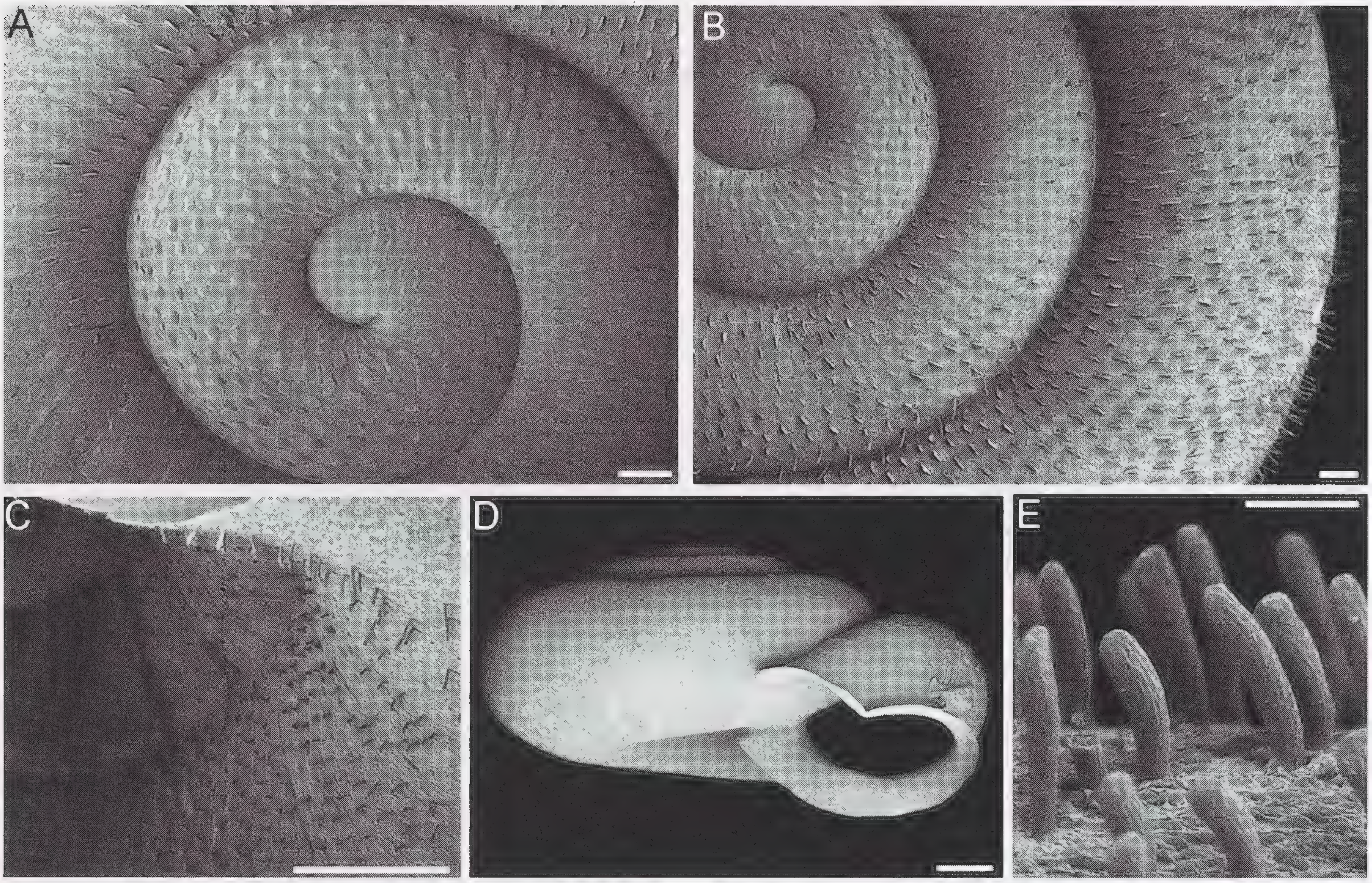

FIG. 138. SEM micrographs of the shell of ***Setobaudinia capillacea*** n. sp. paratype AM C471836 (Boongaree Island). A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above. Scale bars A–B = 200 μm; C: Close-up inner umbilical whorls showing periostracal granules. Scale bar = 500 μm; D: Shell, frontal view showing aperture. Scale = 1 mm; E: Close-up showing periostracal hairs on mid-portion of last whorl. Scale bar = 50 μm.

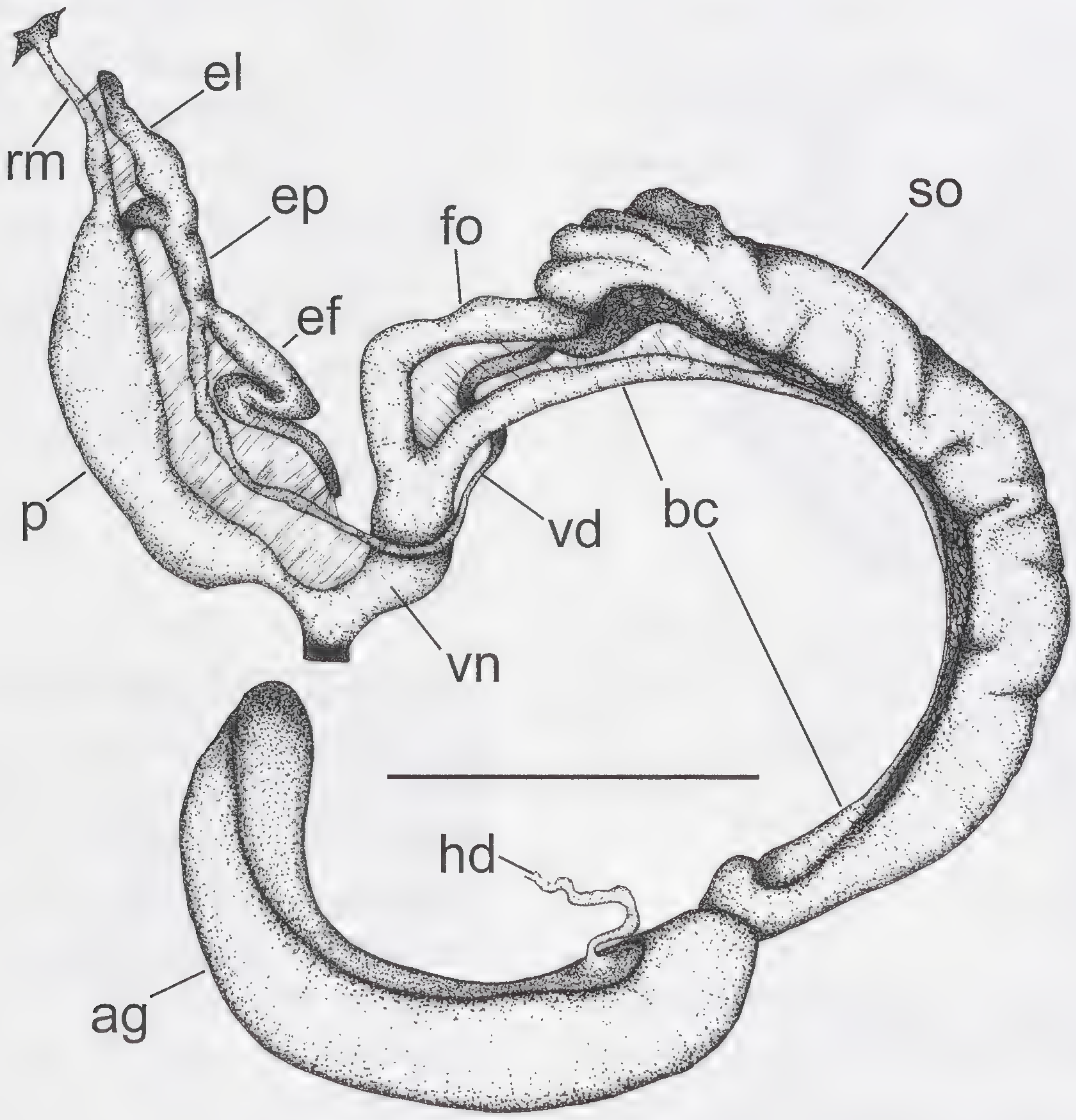

FIG. 139. Genital anatomy of ***Setobaudinia capillacea*** n. sp. holotype WAM 58477 (Boongaree Island, August). Scale bar = 3 mm.

that are arranged in parallel radial rows with their broadest side facing direction of coiling (Fig. 138B). These extensions are replaced by short, blunt, thick periostracal hairs on last whorl from periphery downward into umbilicus. Sculpture also comprises microscopic granules on entire shell being more pronounced underneath suture. Extensions, hairs and granules may be worn in adults. Last whorl weakly descending behind aperture, slightly kinked immediately behind lip; angle of aperture ~ 60°; aperture wide, with sharp, weakly expanded and reflected lip, slightly flattened at base, basal node weak or absent; palatal portion of lip slightly intended, parietal wall delicate.

Genital anatomy (Figs. 139–140): Penis longer than vagina, straight. Epiphallus as long as penis, with very long epiphallic flagellum and long epiphallic lobe. Interior penial wall completely covered with densely packed, transverse lamellar pilasters, proximally being replaced by laterally elongated pustules. Penial verge large. Penial retractor muscle short. Vagina about same length as free oviduct, tubular to posteriorly expanded.

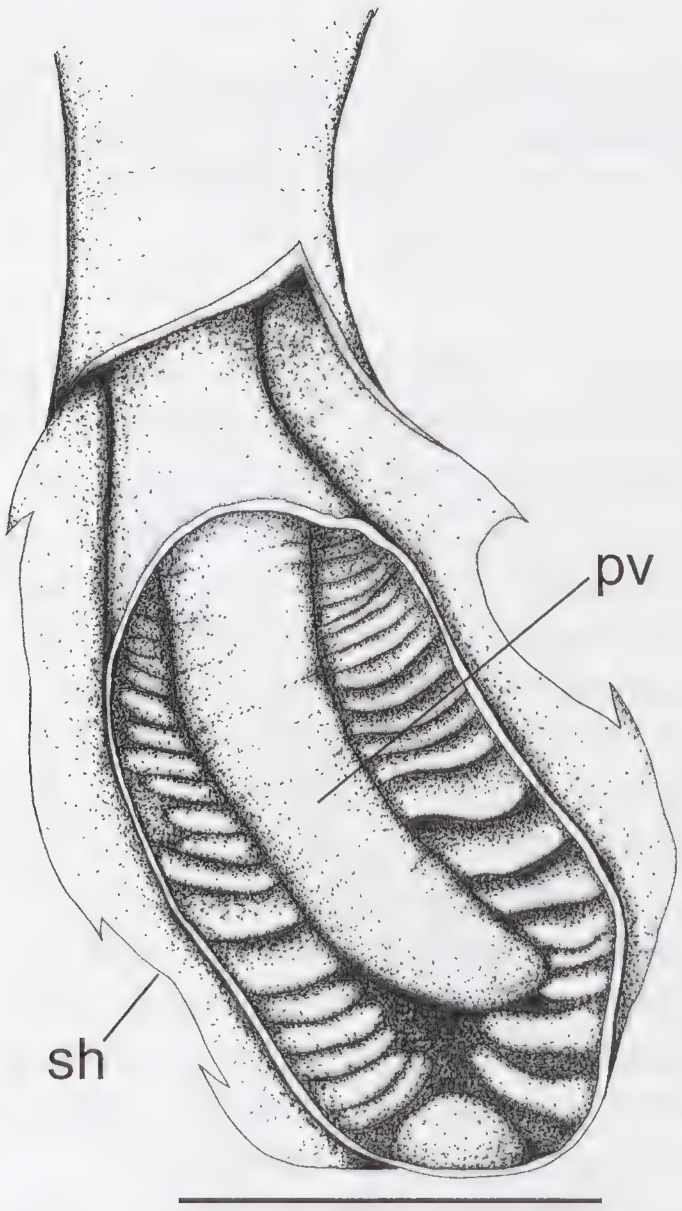

FIG. 140. Penial anatomy of ***Setobaudinia capillacea*** n. sp. holotype WAM 58477 (Boongaree Island, August). Scale bar = 1 mm.

Mitochondrial Differentiation

Infraspecific genetic distances (2 sequences): 0.007; interspecific genetic distances: 0.154–0.182 to all remaining congeners (33 sequences, 12 species).

Comparative Remarks

Shell slightly larger and proportionally higher than ***S. ngurraali***, ***S. umbadayi***, and ***S. wuyurru***. Microsculpture of triangular periostracal extensions and short, blunt, thick periostracal hairs on base of shell typical.

Distribution (Fig. 122)

Boongaree Island.

Setobaudinia garlinju n. sp.

Figs. 123H, 141–144

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, N section of Coronation Island, 14°58'30"S, 124°54'31"E; coll. Vince Kessner, 27/05/2008, KIS 3–72 (vine thicket on steep lower slopes with skeletal soil; large volcanic rocks; under rocks in loose soil).

Material Examined

Holotype WAM S58478 (preserved specimen, dissected). Paratypes WAM S37045 (7 preserved specimens), AM C471839 (18 shells), AM C471840 (20 shells), WAM S37366 (20 shells), WAM S37047 (11 preserved specimens), WAM S37368 (32 shells) from northern section of Coronation Island.

Additional, non-type material. WAM S37039 – WAM S37044, WAM S37046, WAM S37048 (preserved specimens), AM C471841, WAM S37359 – WAM S37365, WAM S37367, WAM S37369 (shells) from northern section of Coronation Island; AM C471842, WAM S37049 – WAM S37055 (preserved specimens), AM C471843, WAM S37370 – WAM S37379 (shells) from southern section of Coronation Island.

Etymology

For Garlinju, name of Coronation Island in Wunambal, language of the Uunguu people; noun in apposition.

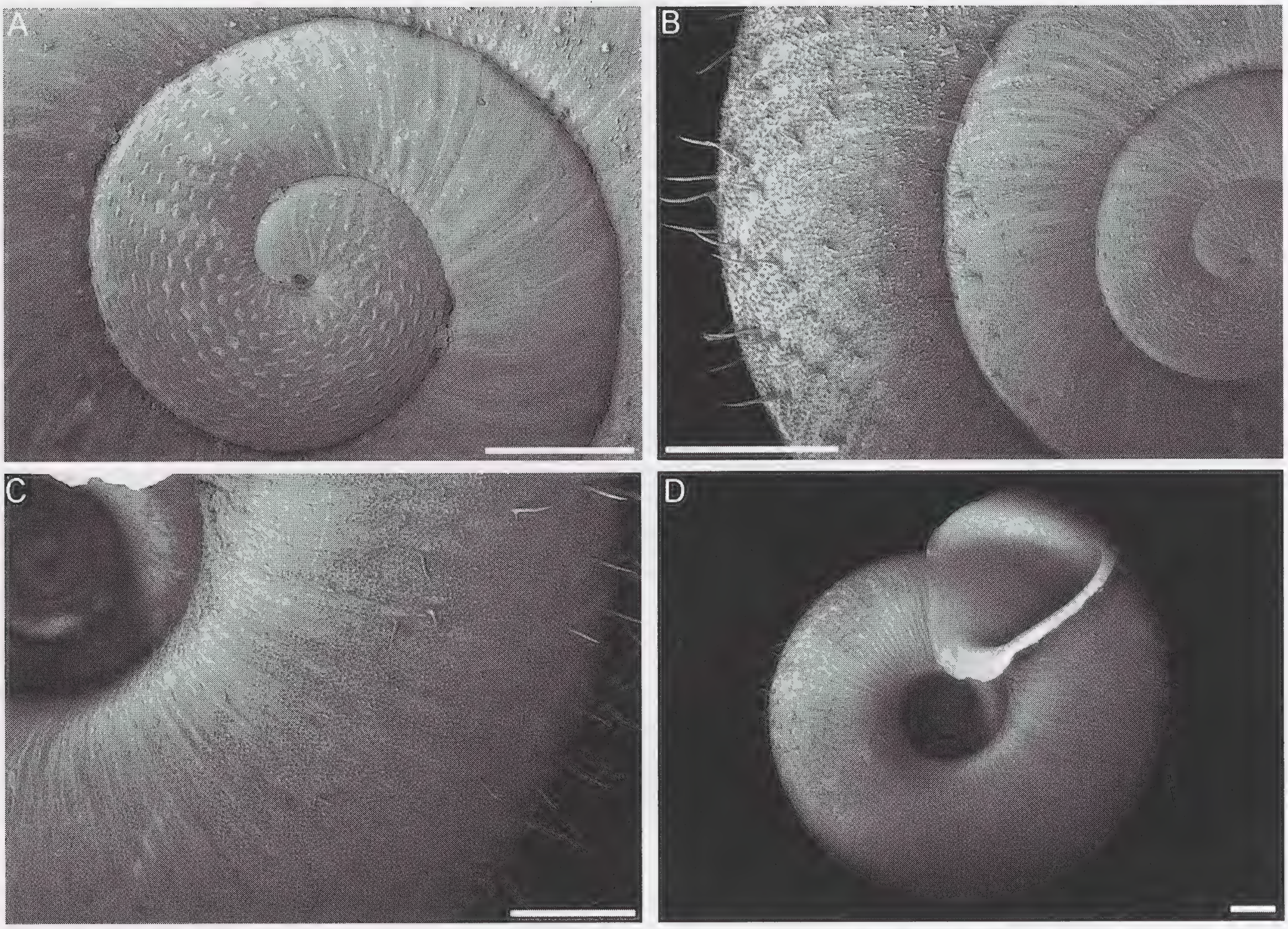

FIG. 141. SEM micrographs of the shell of ***Setobaudinia garlinju*** n. sp. paratype AM C471840 (Coronation Island). A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Umbilical view; D: Shell from below showing aperture. Scale bars B–D = 1 mm.

Description

Shell (Figs. 123H, 141). Small (D = 8.3 mm on average; Table 9), with weakly to moderately elevated spire; periphery angulated; umbilicus on average 1.9 mm wide; colour light yellowish brownish. Protoconch ~ 1.4 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell sparsely covered with radially arranged, pointed periostracal hairs (usually worn off in adults), and microscopic wavy axial ridglets. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp, well- to strongly expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin well rounded without indention, parietal wall delicate.

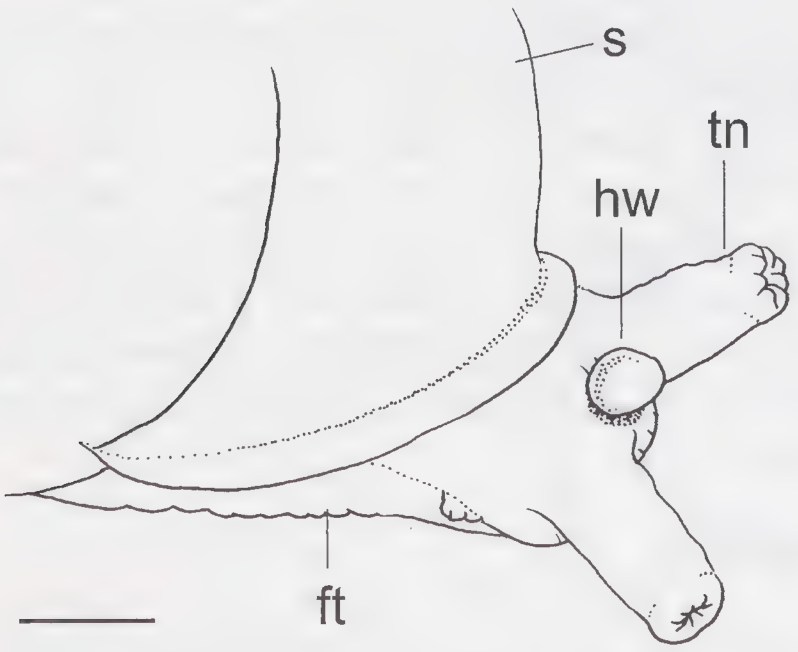

FIG. 142. Head of ***Setobaudinia garlinju*** n. sp. holotype WAM S58478 with eversed head wart. Scale bar = 1 mm.

Genital anatomy and *head wart* (Figs. 142–144). Penis as long as vagina, slightly twisted into S-shape. Epiphallus almost as long as penis, with moderately long epiphallic flagellum and well-developed epiphallic lobe. Distal half of inner penial wall smooth; proximal half completely covered with densely packed, later-

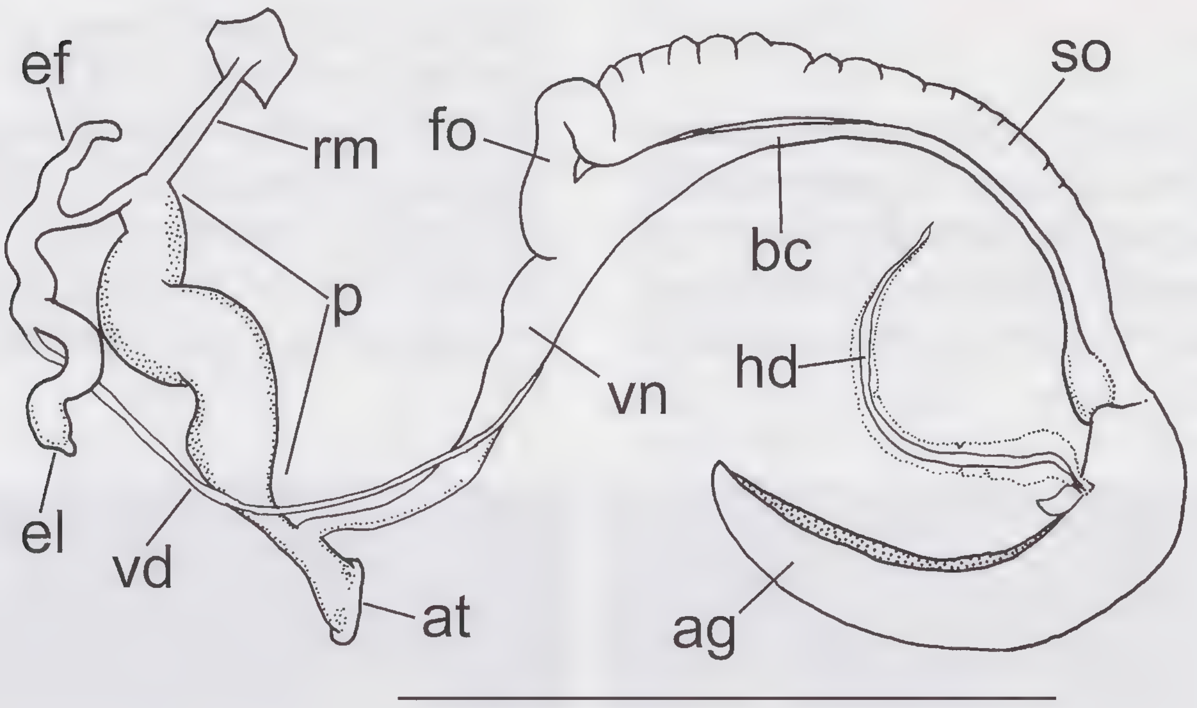

FIG. 143. Genital anatomy of **Setobaudinia garlinju** n. sp. holotype WAM S58478 (Coronation Island, May). Scale bar = 5 mm.

ally strongly elongated pustules, distally being replaced by more rounded, smaller pustules. Penial verge extends about half of length of penial chamber, elongate, thick, with blunt end. Penial retractor muscle comparatively long. Vagina tubular, elongate much longer than free oviduct. Head wart round and smooth (Fig. 142).

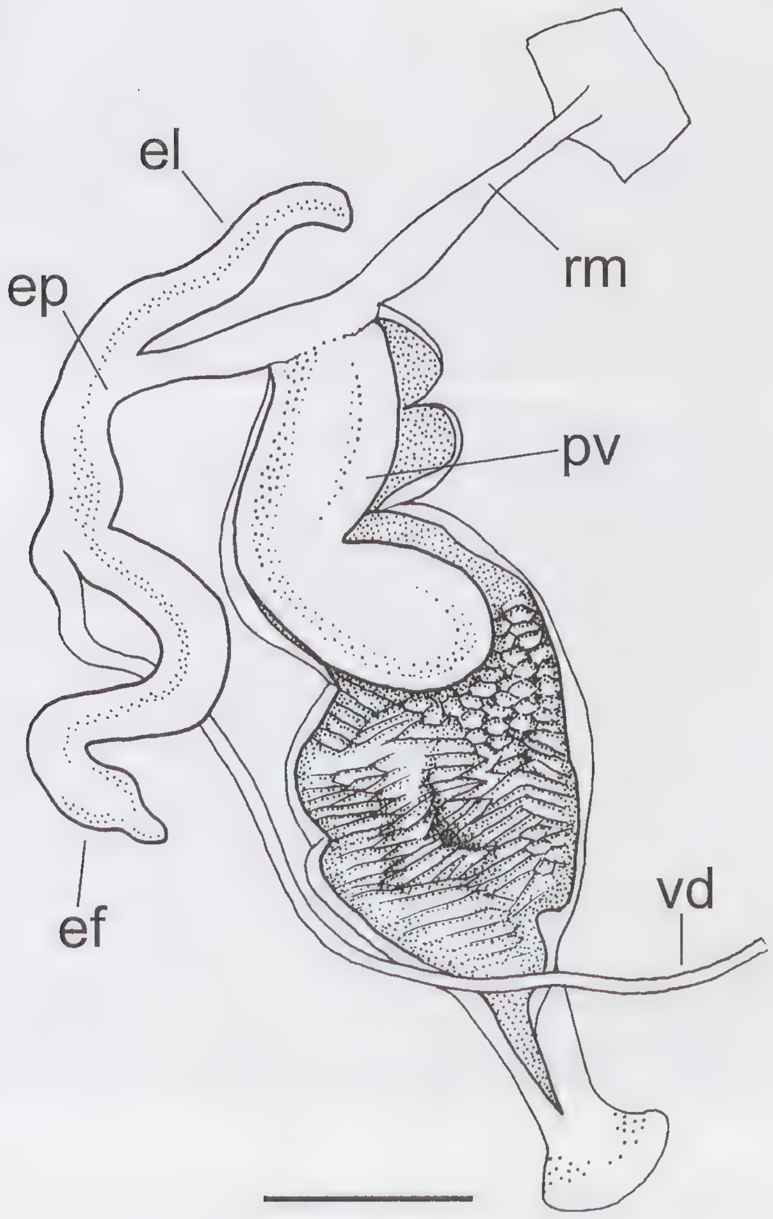

FIG. 144. Penial anatomy of **Setobaudinia garlinju** n. sp. holotype WAM S58478 (Coronation Island, May). Scale bar = 1 mm.

Mitochondrial Differentiation

Infraspecific genetic distances (3 sequences): 0.001–0.01; interspecific genetic distances: 0.13 with respect to ***S. insolita*** (1 sequence), 0.123–0.124 to ***S. gumalamala*** (2 sequences), and 0.158–0.186 to all remaining congeners (29 sequences, 10 species).

Comparative Remarks

One of the smaller species; in contrast to *S. hirsuta*, ***S. ngurraali***, ***S. umbadayi*** and ***S. wuyurana***, last whorl not conspicuously kinked behind aperture. These species also differ in presence of lateral pilasters at inner penial wall rather than laterally elongated pustules. Penial verge of ***S. garlinju*** exceptionally long, microsculpture of shell comparatively inconspicuous with few but long periostracal hairs, pustulation of inner umbilicus comparatively sparse.

Distribution (Fig. 122)

Coronation Island.

Setobaudinia gumalamala n. sp.
Figs. 123I, 145–147

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, St Andrew Island, 15°21’34”S, 124°59’45”E; coll. Roy Teale, 25/05/2008, KIS–042 (sandstone scree on lower slopes under dense woodland; under rocks in loose soil).

Material Examined

Holotype WAM S58479 (preserved specimen, dissected). Paratypes WAM S37032 (2 preserved specimens), WAM S37271 (9 shells) from type locality; WAM S37268 (shell) from 15°21'26"S, 124°59'48"E; WAM S37031 (preserved specimen), WAM S37269 (3 shells) from 15°21'34"S, 125°00'07"E; WAM S37087 (preserved specimen), WAM S37270 (4 shells) from 15°21'34"S, 125°59'59"E; WAM S37272 (4 shells), AM C471844 (2 shells) from 15°21'24"S, 124°59'46"E; WAM S37034 (3 preserved specimens) from 15°21'32"S,

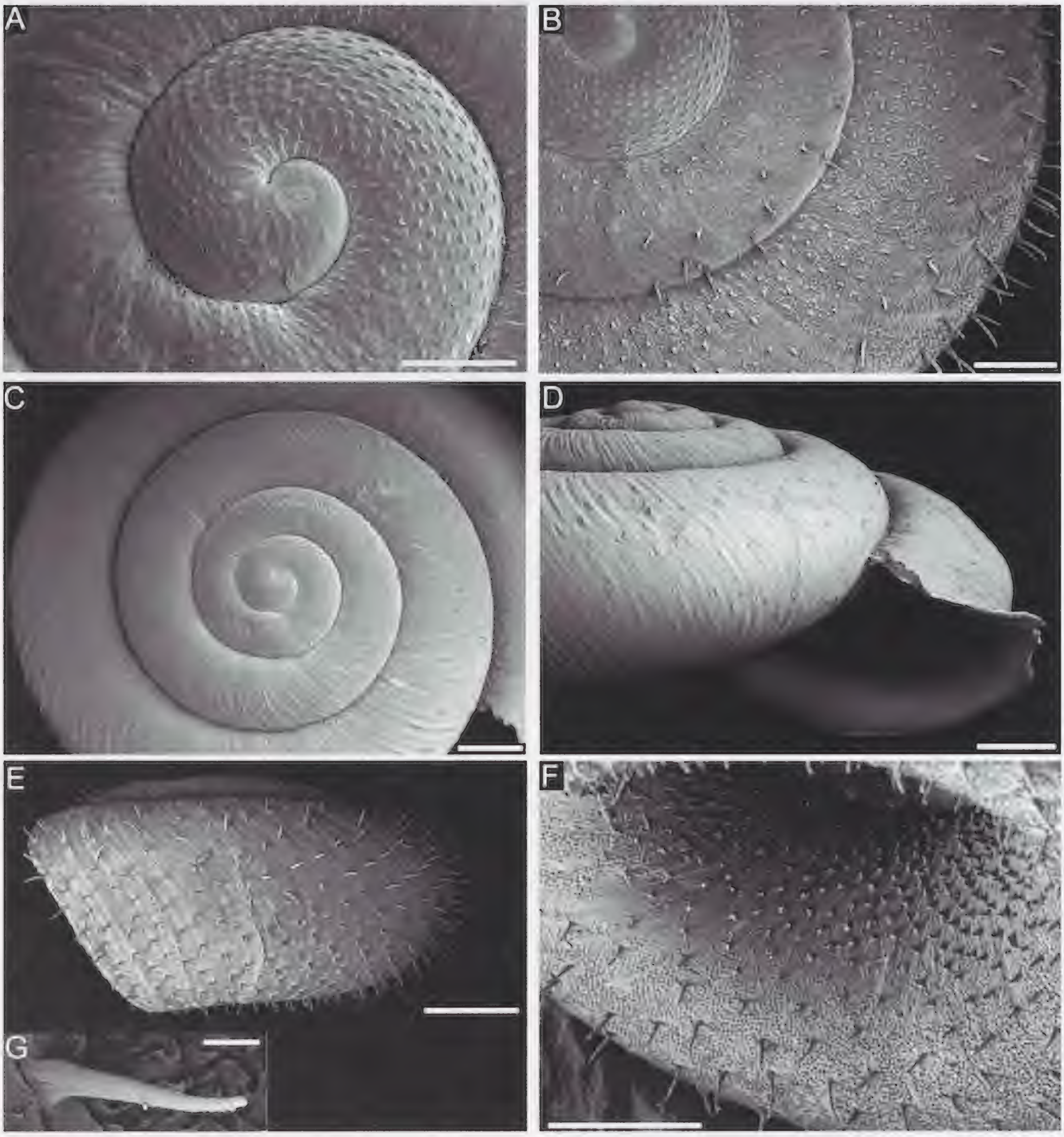

FIG. 145. SEM micrographs of the shell of ***Setobaudinia gumalamala*** n. sp. paratype AM C471844 (St Andrews Island). A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above. Scale bars A–B = 500 µm; C: Entire shell viewed from above; D: Frontal view showing sculpture on last whorl and aperture; E: Sub-adult shell with periostracal hairs. Scale bars C–E = 1 mm; F: Umbilical view showing periostracal hairs and granules. Scale bar = 500 µm; G: Close-up of periostracal hair. Scale bar = 100 µm.

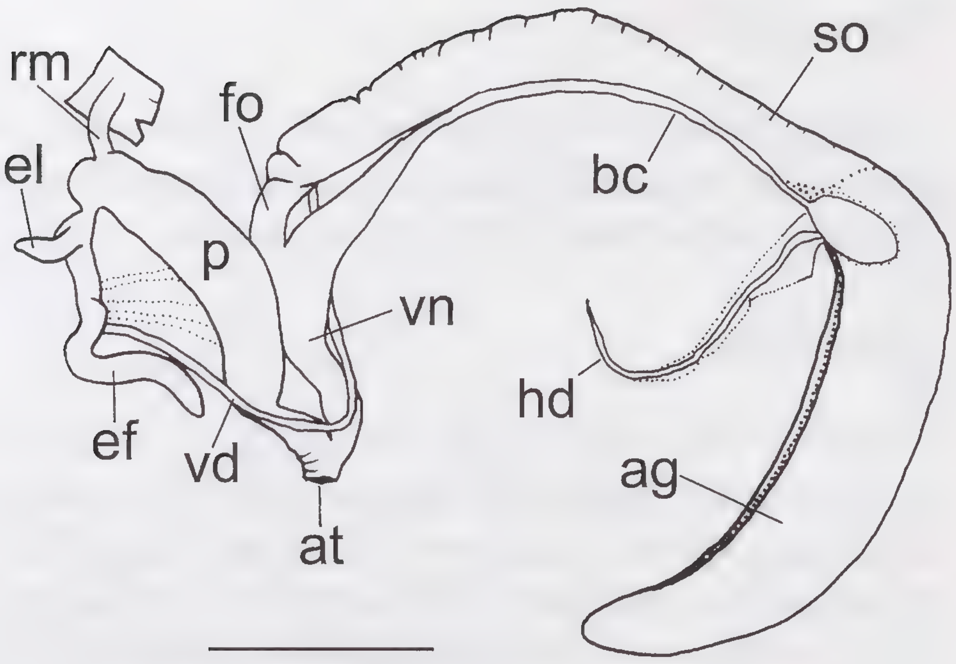

FIG. 146. Genital anatomy of ***Setobaudinia gumalamala*** n. sp. holotype WAM S58479 (St Andrews Island, May). Scale bar = 2 mm.

124°59'52"E; WAM S37033 (preserved specimen), AM C471845 (4 shells), WAM S37273 (6 shells) from 15°21'36"S, 124°59'41"E; WAM S49045 (shell) from 15°21'22.7"S, 124°59'50"E; WAM S37689 (preserved specimen) from 15°21'29.5"S, 124°59'51.1"E.

Etymology

Gumalamala, name of St. George Basin and islands, including St. Andrew Island, in Worrorra, language of the Dambimangari people; noun in apposition.

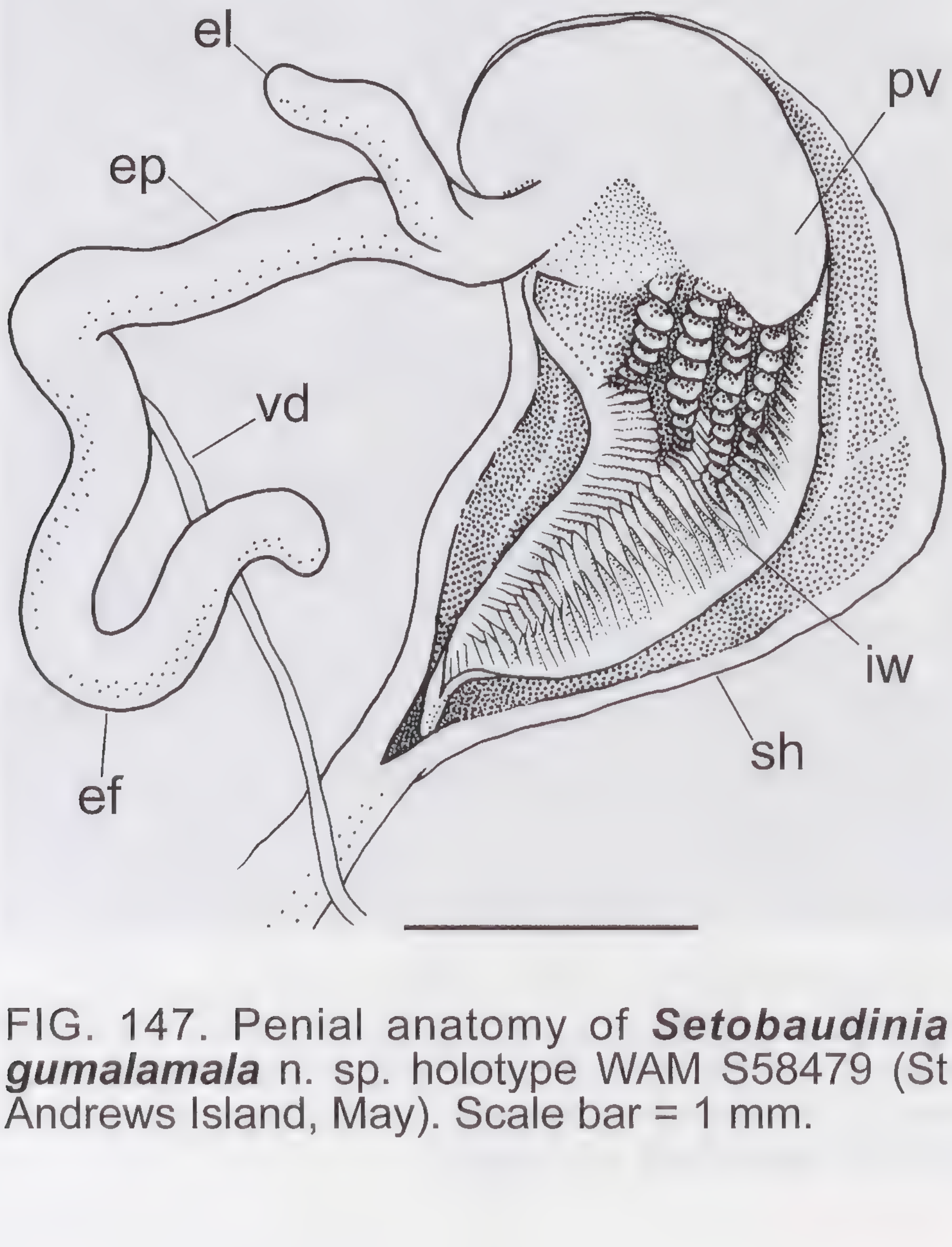

FIG. 147. Penial anatomy of ***Setobaudinia gumalamala*** n. sp. holotype WAM S58479 (St Andrews Island, May). Scale bar = 1 mm.

Description

Shell (Figs. 123I, 145): Small (D = 7.7 mm on average; Table 9), with weakly elevated spire; last whorl, periphery rounded to slightly angulated; umbilicus on average 2.0 mm wide. Protoconch ~ 1.6 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell sparsely covered with radially arranged, pointed periostracal hairs (usually worn in adults), microscopic granules particularly prominent underneath suture and within umbilicus, and wavy axial ridglets. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp, well- to strongly expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin well rounded without indention, parietal wall delicate.

Genital anatomy (Figs. 146–147). Penis twice as long as vagina, rather straight. Epiphallus almost as long as penis, with long epiphallic flagellum and well-developed epiphallic lobe; two longitudinal epiphallic pilasters. Distal quarter of inner penial wall smooth, mid-portion of wall with three longitudinal rows of regularly sized, roundish pustules, proximal half with 3 longitudinal rows of densely packed, interlocking laterally elongated pustules. Anterior end of penis very thin, with weak walls. Penial verge extends about one quarter of length of penial chamber, thick, blunt. Penial retractor muscle short. Vagina tubular, elongate, about same length as free oviduct. Free oviduct moderate in length, rather straight.

Mitochondrial Differentiation

Infraspecific genetic distances (2 sequences): 0.003; interspecific genetic distances: 0.05 with respect to ***S. insolita*** (1 sequence), 0.123–0.124 to ***S. garlinju*** (2 sequences), and 0.158–0.186 to all remaining congeners (29 sequences, 10 species).

Comparative Remarks

One of the smallest species; compared to *S. hirsuta*, ***S. ngurraali***, ***S. umbadayi*** and ***S. wuyurana***, last whorl not conspicuously kinked behind aperture. These species also differ in presence of lateral pilasters at inner penial wall rather than laterally elongated pustules. Compared to ***S. garlinju*** vagina much longer, penial verge much shorter, pustulation of inner umbilicus more crowded.

Distribution (Fig. 122)

St. Andrew Island.

Setobaudinia insolita n. sp.
Figs. 123J, 148–150

Type Locality

Western Australia, central Kimberley coast, Saint George Basin, St. Patrick Island, 15°21'23"S, 124°57'55"E; coll. Vince Kessner, 09/02/2009, KIS 2–64 (vine thicket on steep slopes, sandstone boulders; under rocks).

Material Examined

Holotype WAM S37690 (preserved specimen, dissected). Paratypes AM C471846 (6 shells), WAM S49044 (12 shells) from type locality.

Etymology

Derived from "*insolitus*" (Latin, masculine = unfamiliar, strange) for its unusual penial morphology; adjective of feminine gender.

Description

Shell (Figs. 123J, 148): Small (D = 8.3 mm on average; Table 9), with weakly elevated spire; last whorl, periphery rounded to slightly angulated; umbilicus on average 2.1 mm wide. Protoconch ~ 1.5 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell densely covered with radially arranged, rather short periostracal hairs (may be worn off in adults), microscopic granules, particularly prominent underneath suture and within umbilicus, and wavy axial ridglets. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp,

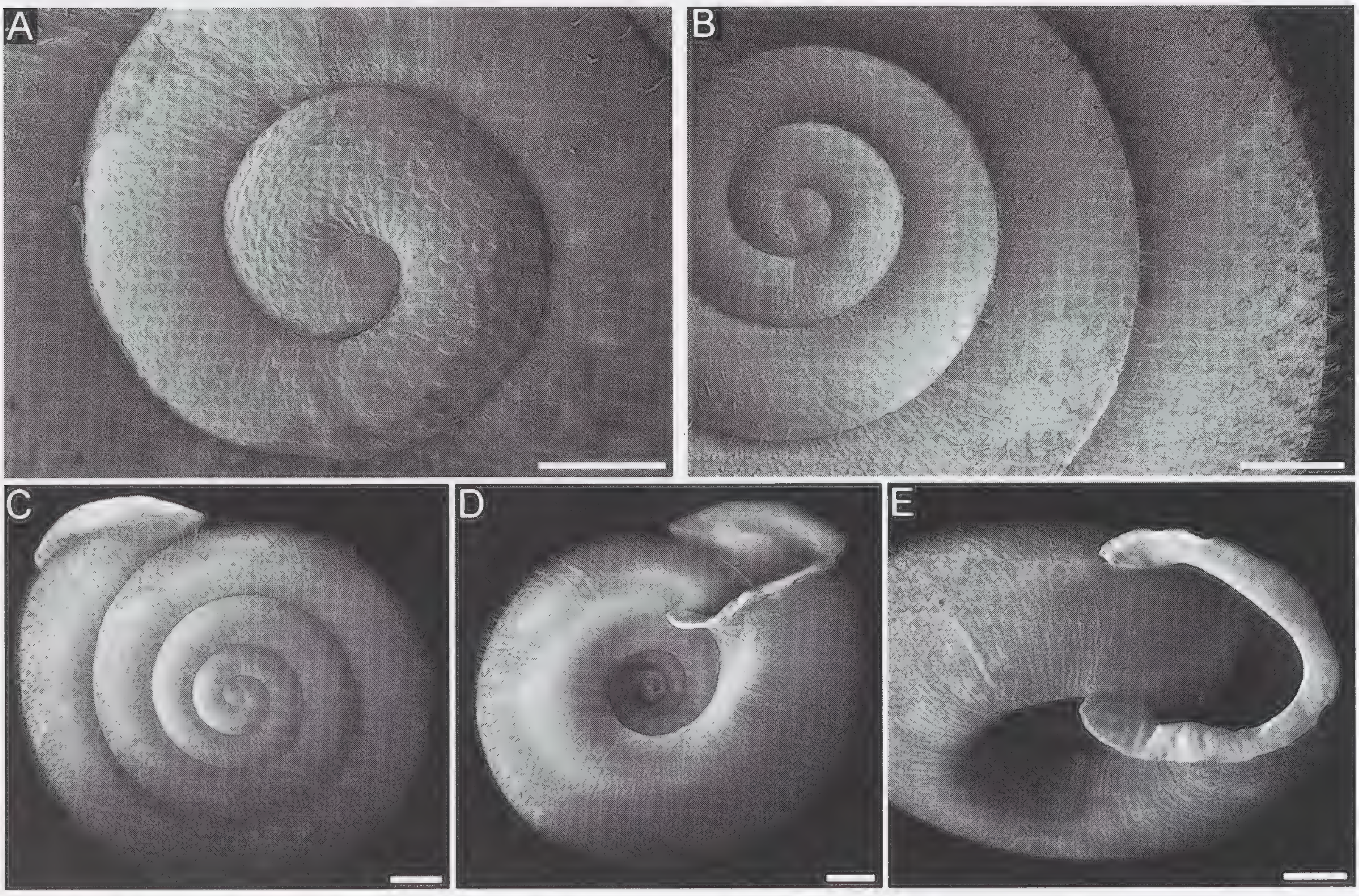

FIG. 148. SEM micrographs of the shell of ***Setobaudinia insolita*** n. sp. paratype AM C471846 (St Patrick Island). A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Entire shell viewed from below; E: Entire shell viewed obliquely from below showing aperture. Scale bars C–E = 1 mm.

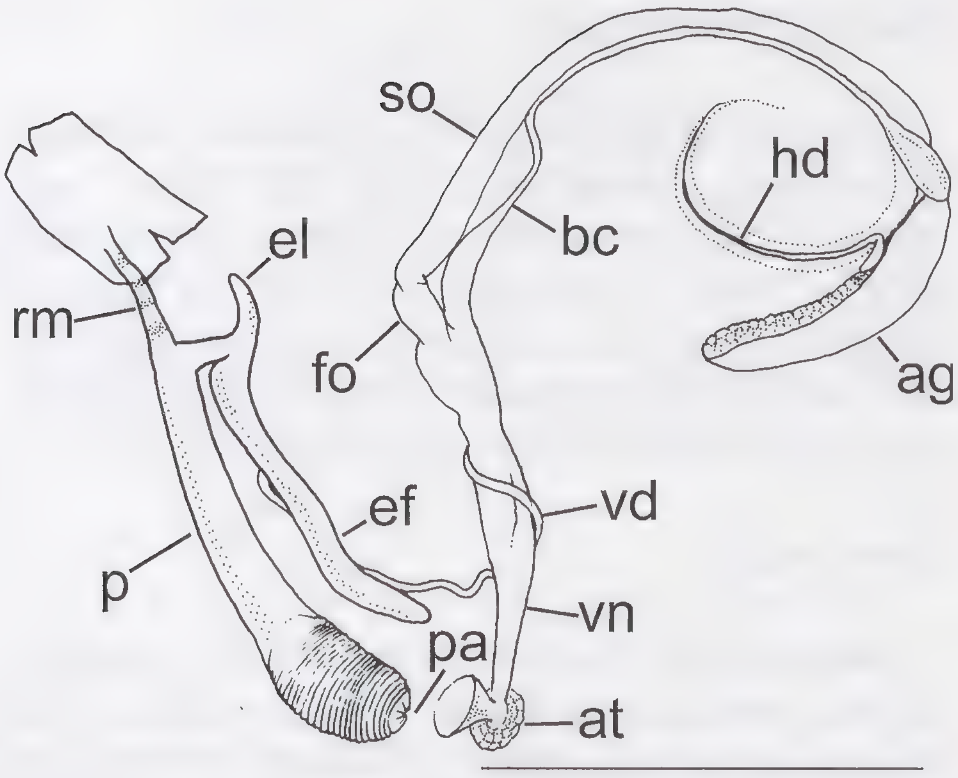

FIG. 149. Genital anatomy of ***Setobaudinia insolita*** n. sp. holotype WAM S37690 (St Patrick Island, February). Scale bar = 5 mm.

well- to strongly expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin not or weakly indented, parietal wall delicate.

Genital anatomy (Figs. 149–150): Penial complex very long (about as longs as vagina, which is also very long), tubular and thin within thick penial sheath, rather straight. Epiphallus almost as long as penis, reflecting into penial sheath as simple thin tube, with very long epiphallic flagellum and well-developed epiphallic lobe; penis proper restricted to proximal quarter of entire length of penial complex. Penial verge situated at extremely anterior position with respect to entire length of penial complex, tongue-shaped with slit-like opening. Penis proper coiled; inner wall with complex, interlocking, elongated pilasters. In illustrated specimen, penis entirely detached from atrium. Vagina tubular, much longer than free oviduct.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.05 with respect to ***S. gumalamala*** (2 sequences), 0.13 to ***S. garlinju*** (2 sequences), and 0.158–0.186 to all remaining congeners (29 sequences, 10 species).

Comparative Remarks

One of the smallest species of the genus; in contrast to *S. hirsuta*, ***S. ngurraali***, ***S. umbadayi*** and ***S. wuyurana***, last whorl not conspicuously kinked behind aperture. Most conspicuous features are penis with reflexing epiphallus, proximally located, tongue-like penial verge, and short penis proper with complex

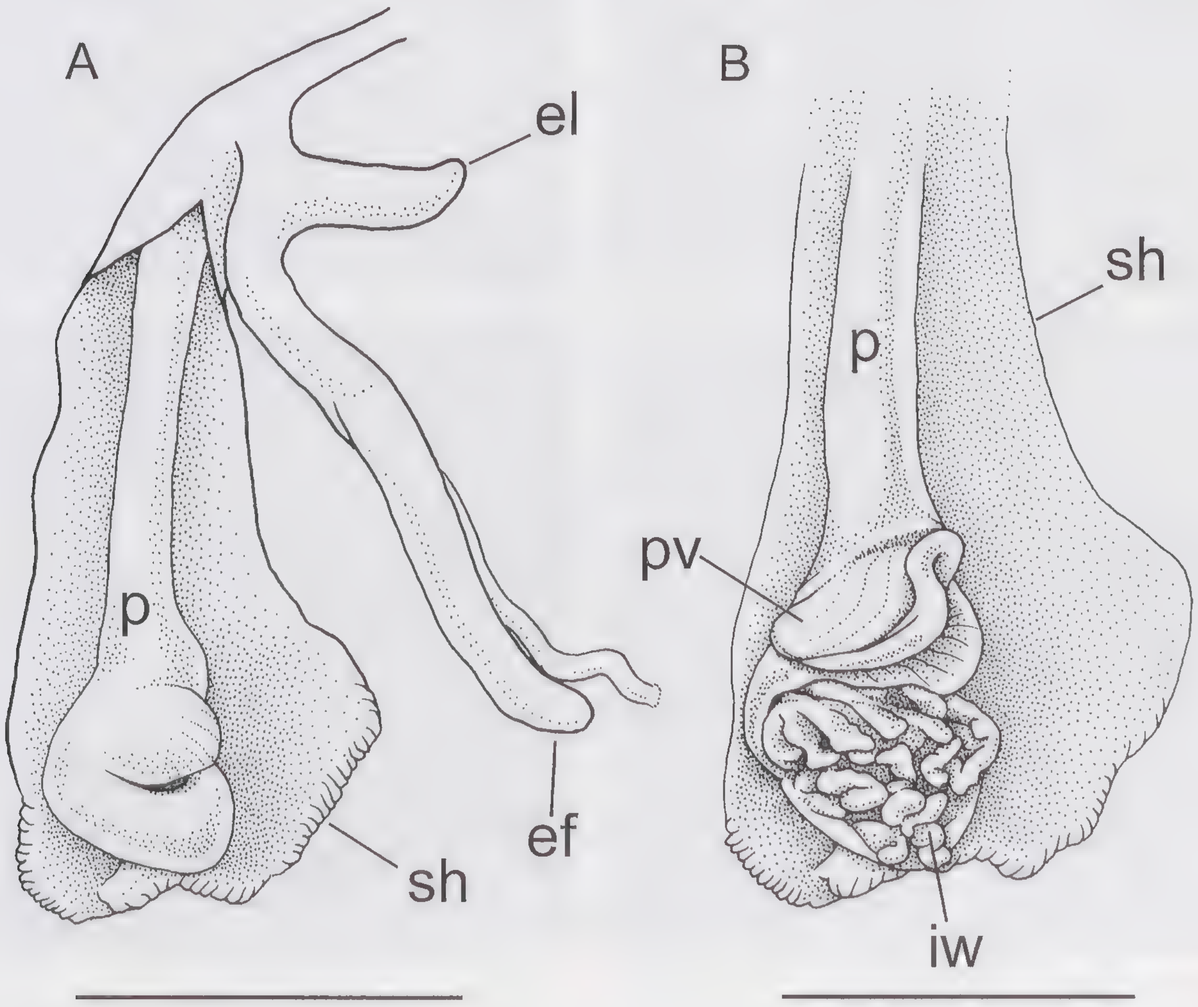

FIG. 150. Penial anatomy of ***Setobaudinia insolita*** n. sp. holotype WAM S37690 (St Patrick Island, February). A: Penis within opened penial sheath. Scale bar = 2 mm; B: Internal penial anatomy showing penial verge and complex penial wall pustulation. Scale bar = 1 mm.

interlocking penial wall pilaster plus extremely long vagina. It is not known whether complete detachment of penis is typical for this species. This feature is found also in other species, possibly depending on reproductive or developmental status of specimen.

Distribution (Fig. 122)

St. Patrick Island.

Setobaudinia quinta n. sp.

Figs. 123K, 151–153

Type Locality

Western Australia, southwestern Kimberley, Doubtful Bay, SE section of Storr Island, 15°56'54"S, 124°33'32"E; coll. Vince Kessner, 24/05/2009, KIS 3–148 (large rocky outcrop in vine thicket at base of sandstone cliffs; under rocks in loose soil).

Material Examined

Holotype WAM S58480 (preserved specimen, dissected). Paratypes WAM S37729 (3 preserved specimens), WAM S37891 (17 shells), AM C471847 (10 shells), WAM S37794 (2 preserved specimens), WAM S37889 (50 shells), AM C471848 (23 shells), WAM S37890 (shell), WAM S37888 (4 shells) from type locality.

Etymology

Derived from "*quinta*" (Latin = fifth), referring to the manuscript name "*Setobaudinia* NSP 5" used by Solem (1991) for material from the Doubtful Bay area and further south, which is believed to be at least in part conspecific.

Description

Shell (Figs. 123K, 151): Small (D = 6.7 mm on average; Table 9), nearly discoidal with weakly

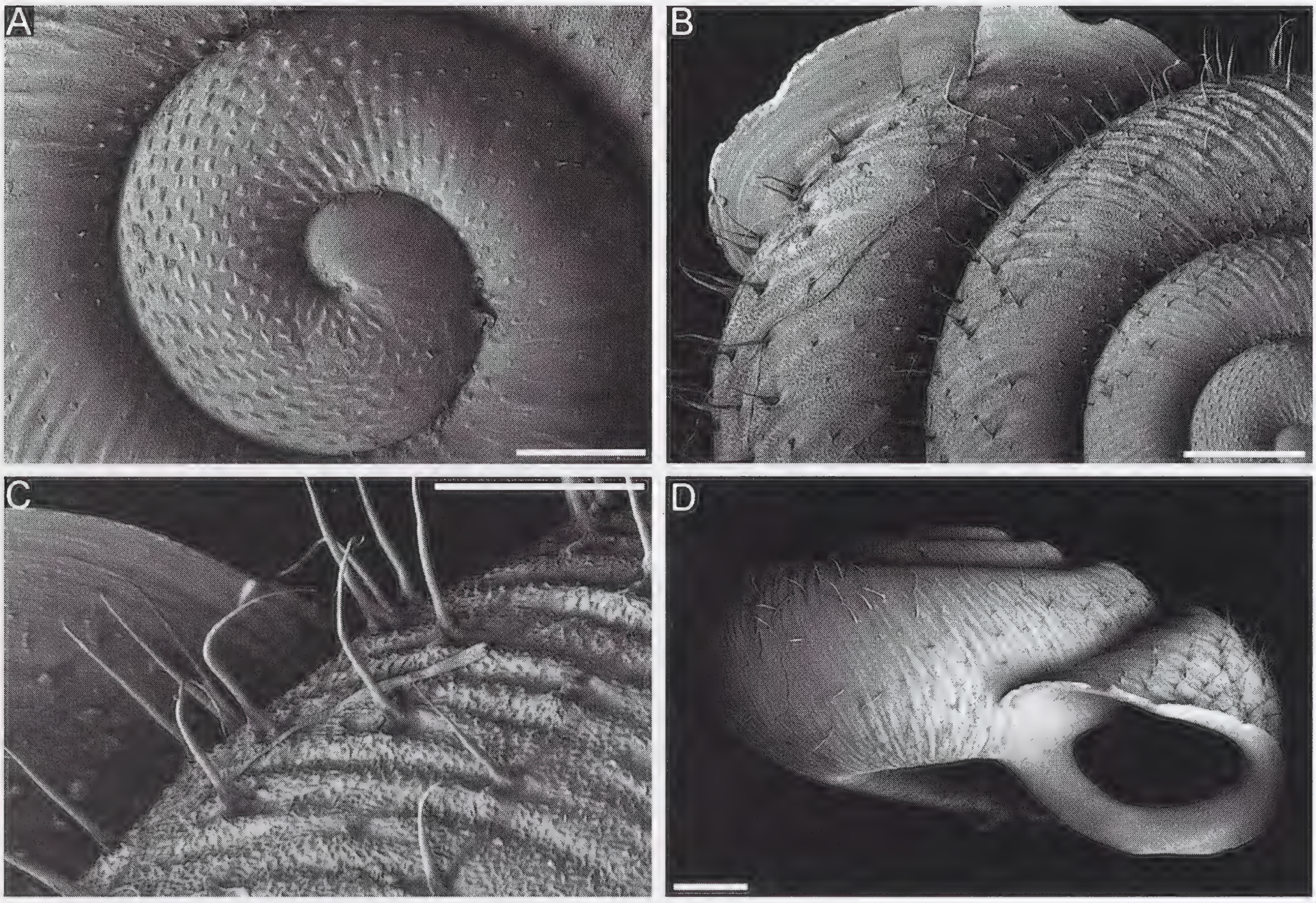

FIG. 151. SEM micrographs of the shell of ***Setobaudinia quinta*** n. sp. paratype AM C471847 (Storr Island). A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above; C: Close-up of periostracal hairs on penultimate whorl; D: Frontal view of entire shell showing aperture. Scale bars A, C = 500 μm; B, D = 1 mm.

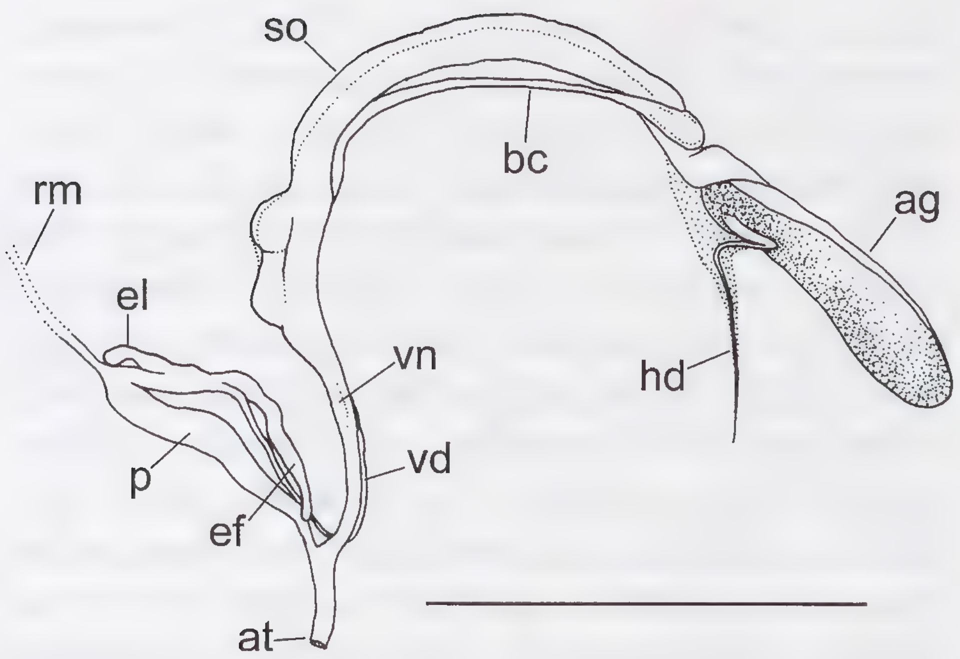

FIG. 152. Genital anatomy of ***Setobaudinia quinta*** n. sp. holotype WAM S58480 (Storr Island, May). Scale bar = 5 mm.

elevated spire; periphery rounded to slightly angulated; umbilicus on average 1.7 mm wide, not concealed; colour light yellowish brownish. Protoconch about 1.6 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with almost invisible, faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell sparsely covered with radially arranged, pointed and thin periostracal hairs (usually worn in adults), microscopic granules particularly prominent underneath suture and within umbilicus. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp, moderately expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin not or weakly indented, parietal wall delicate.

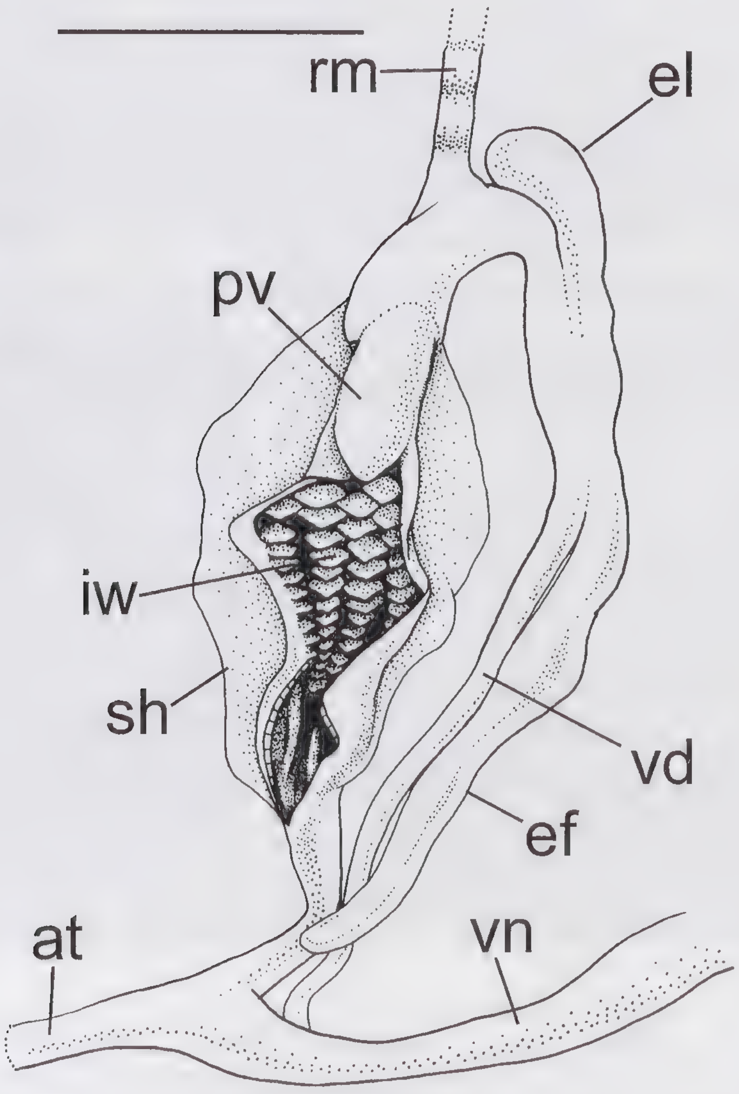

FIG. 153. Penial anatomy of ***Setobaudinia quinta*** n. sp. holotype WAM S58480 (Storr Island, May). Scale bar = 1 mm.

Genital anatomy (Figs. 152–153): Penis moderately long (about same length as vagina), rather straight. Epiphallus almost as long as penis, with moderately long epiphallic flagellum and well-developed epiphallic lobe; interiorly with one thin longitudinal epiphallic pilaster. Inner penial wall with longitudinal rows of triangular pustules that taper in size towards proximal end, giving rise to thin longitudinal pilasters at proximal end of penial wall. Penial verge extending about one quarter of length of penial chamber, thick, blunt. Vagina tubular, elongate, longer than free oviduct.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.004; interspecific genetic distances: 0.155–0.186 to all congeners (33 sequences, 12 species).

Comparative Remarks

Smallest species of the genus. Shell with indistinct axial ribbing and comparatively sparse pustulation. Characteristic penial wall anatomy with longitudinal rows of triangular pustules that taper in size.

Distribution (Fig. 122)

Storr Island and likely adjacent areas on mainland at Doubtful Bay.

Setobaudinia joycei n. sp.

Figs. 123L, 154–156

Type Locality

Western Australia, southwestern Kimberley, Collier Bay, Wulalam Island, 16°22’13.4”S, 124°13’46.7”E; coll. Sean Stankowski, 22/05/2009, KIS 2–73 (cliff face with scree, base of creek line, in leaf litter between rocks).

Material Examined

Holotype WAM S58481 (preserved specimen). Paratypes WAM S37780 (12 preserved specimens), WAM S37779 (7 preserved specimens), AM C471849 (5 preserved specimens), WAM S37884 (8 shells), WAM S37885 (5 shells), AM C471850 (5 shells), WAM S37781 (7 preserved specimens), WAM S37782 (4 preserved specimens), WAM S37886 (3 shells), WAM S37783 (preserved specimen, dissected), WAM S49265 (3 preserved specimens) from Wulalam Island.

Etymology

Named in honour of my friend Michael Joyce (Sydney), who runs the most wonderful barber shop in town; noun in genitive case.

Description

Shell (Figs. 123L, 154): Small (D = 8.3 mm on average; Table 9), nearly discoidal with weakly elevated spire; periphery rounded to slightly angulated; umbilicus on average 2.5 mm wide, not concealed; colour light yellowish brownish. Protoconch about 1.5 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell sparsely covered with radially arranged, pointed periostracal hairs (usually worn off in adults), microscopic granules, particularly prominent underneath suture and within umbilicus. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp, moderately expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin weakly indented, parietal wall delicate.

Genital anatomy (Figs. 155–156): Penis extremely long and thick (twice as long as vagina), coiled within diaphanous penial sheath. Epiphallus almost as long as penis, attached to penis by connective tissue, with comparatively

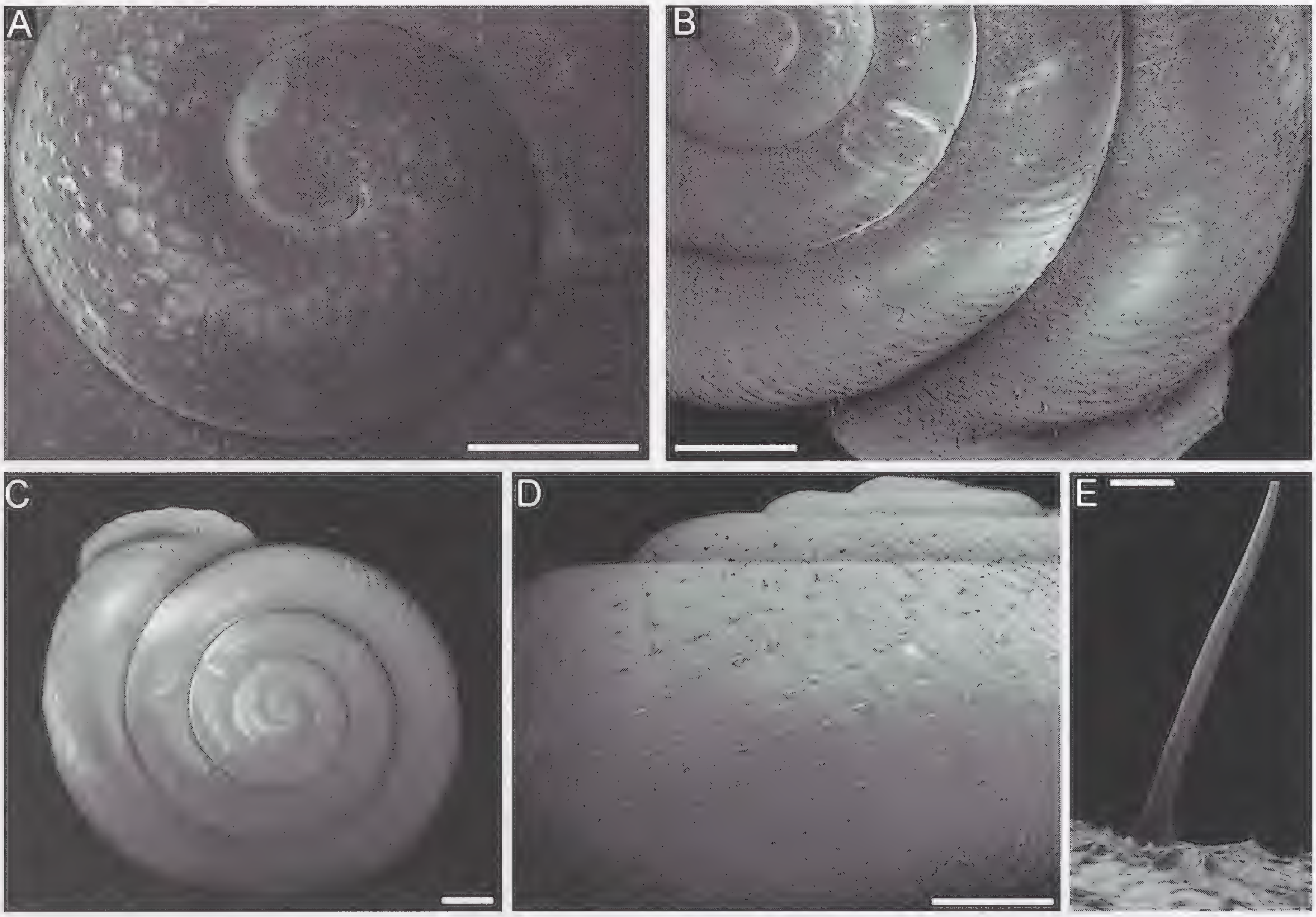

FIG. 154. SEM micrographs of the shell of ***Setobaudinia joycei*** n. sp. paratype AM C471850 (Wulalam Island). A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Lateral view of last whorl showing distribution of periostracal hairs across whorl surface. Scale bars B–D = 1 mm; E: Close-up of periostracal hair. Scale bar = 100 µm.

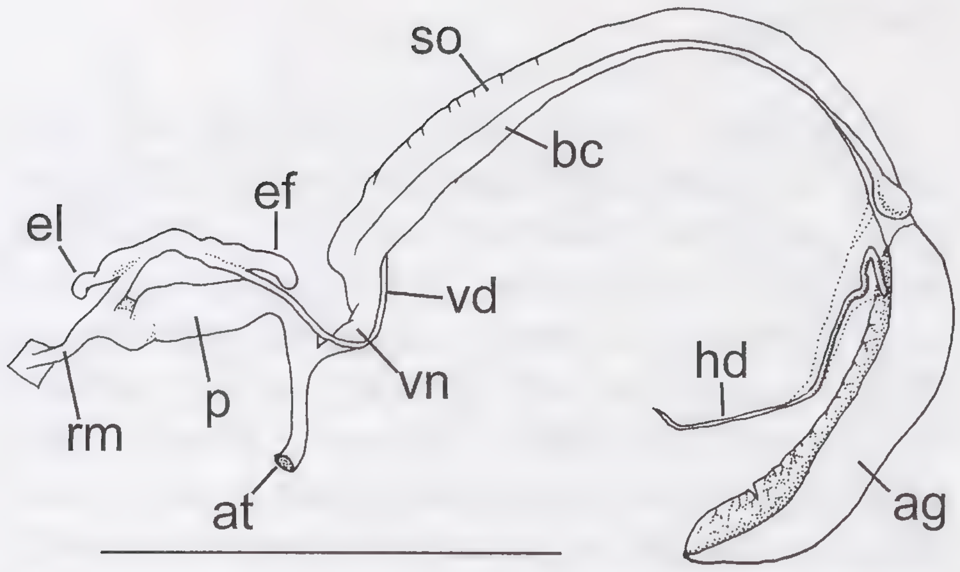

FIG. 155. Genital anatomy of ***Setobaudinia joycei*** n. sp. holotype WAM S58481 (Wulalam Island, May). Scale bars = 3 mm.

short epiphallic flagellum and epiphallic lobe; interiorly with one thick longitudinal epiphallic pilaster. Inner penial wall with very indistinct, obliquely transverse pilasters. Penial verge extends about one third penial chamber, thick, conical. Vagina tubular, elongate, short, longer than free oviduct.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.006; interspecific genetic distances: 0.064–0.70 with respect to ***S. karczewski*** (3 sequences), 0.155–0.182 to all congeners (30 sequences, 11 species).

Comparative Remarks

Illustrated dissection with conspicuously elongated atrium. However, atrium was much shorter in second dissected specimen. Typical for this species is comparative large size of penis, coiling within penial sheath and oblique sculpture of inner penial wall (absence of pustules or lamellae). In addition, relatively widely spaced and sparsely distributed periostracal hairs are typical. When not worn, hairs are comparatively long.

Distribution (Fig. 122)

Wulalam Island.

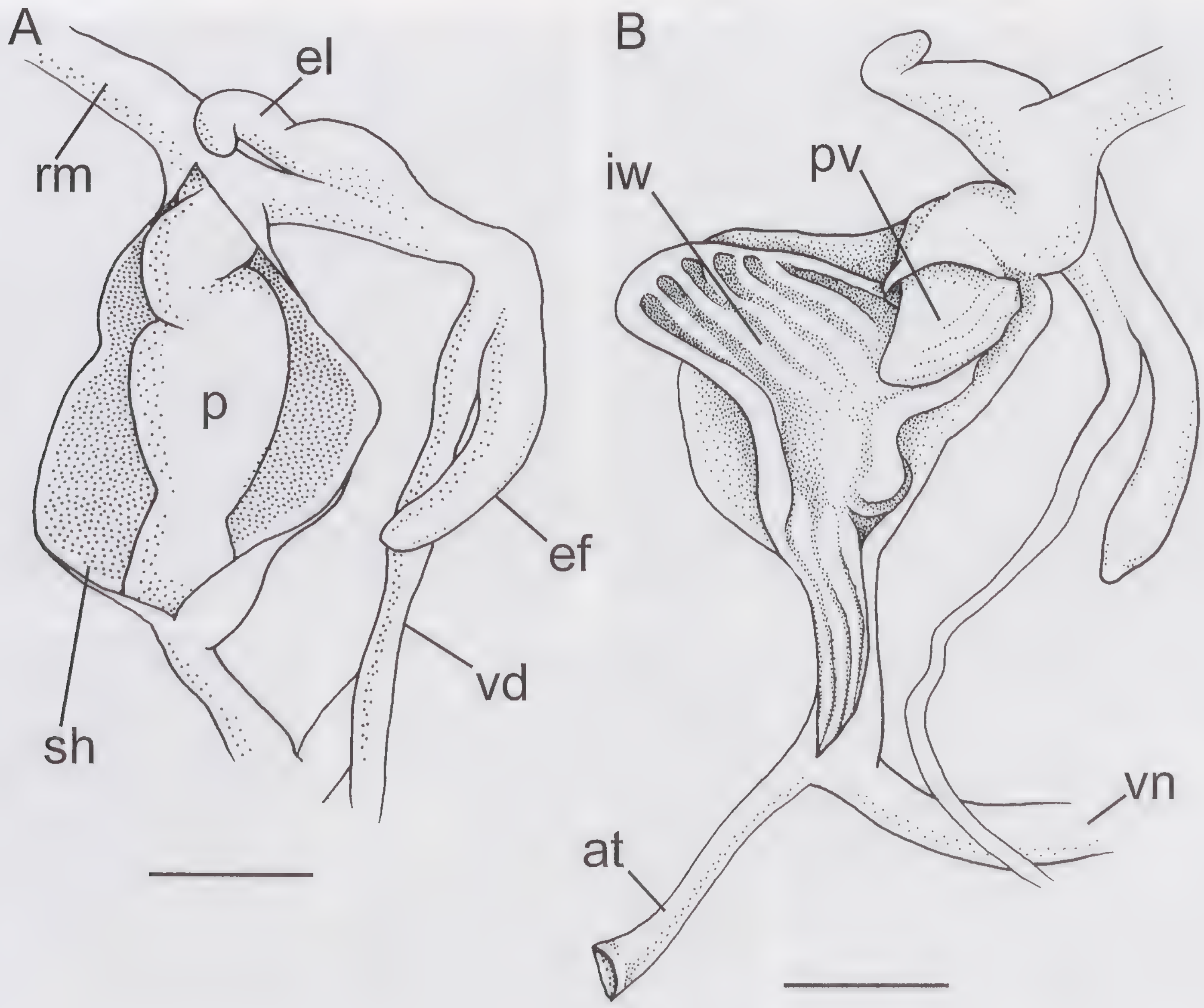

FIG. 156. Penial anatomy of ***Setobaudinia joycei*** n. sp. holotype WAM S58481 (Wulalam Island, May). A: Penis within opened penial sheath; B: Internal penial anatomy showing penial verge and inner wall sculpture. Scale bars = 1 mm.

Setobaudinia karczewski n. sp.

Figs. 123M, 157–159

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, Talbot Bay, N section of Molema Island, 16°15'09.7"S, 123°49'11.7"E; coll. Sean Stankowski, 27/05/2009, KIS 2–79 (rock scree in gully with vine thicket elements; between rocks in soil and litter).

Material Examined

Holotype WAM S58482 (preserved specimen, dissected). Paratypes WAM S37784 (7 preserved specimens), WAM S37887 (3 shells), WAM S49266 (6 preserved specimens), AM C471851 (5 preserved specimens) from N section of Molema Island.

Etymology

Named in honour of Elke Karczewski (Berlin); noun in apposition.

Description

Shell (Figs. 123M, 157): Small (D = 8 mm; Table 9), nearly discoidal with weakly elevated spire; periphery rounded to slightly angulated; umbilicus 1.5 mm wide, not concealed. Protoconch about 1.5 mm in diameter, comprising about one whorl, with regular, strong, radially arranged pustulation. Teleoconch with faint radial growth lines extending onto base of shell and into umbilicus, inner umbilical whorls with periostracal granules, shell sparsely covered with radially arranged, pointed periostracal hairs (usually worn in adults), microscopic granules, particularly prominent underneath suture and within umbilicus. Last whorl weakly to moderately descending behind aperture; angle of aperture 45–60°; aperture wide, with sharp, moderately expanded, weakly reflected lip, flattened at base, basal node weak or absent; palatal margin weakly indented, parietal wall delicate.

Genital anatomy (Figs. 158–159): Penis moderately long (about same length as vagina), straight. Epiphallus almost as long as penis,

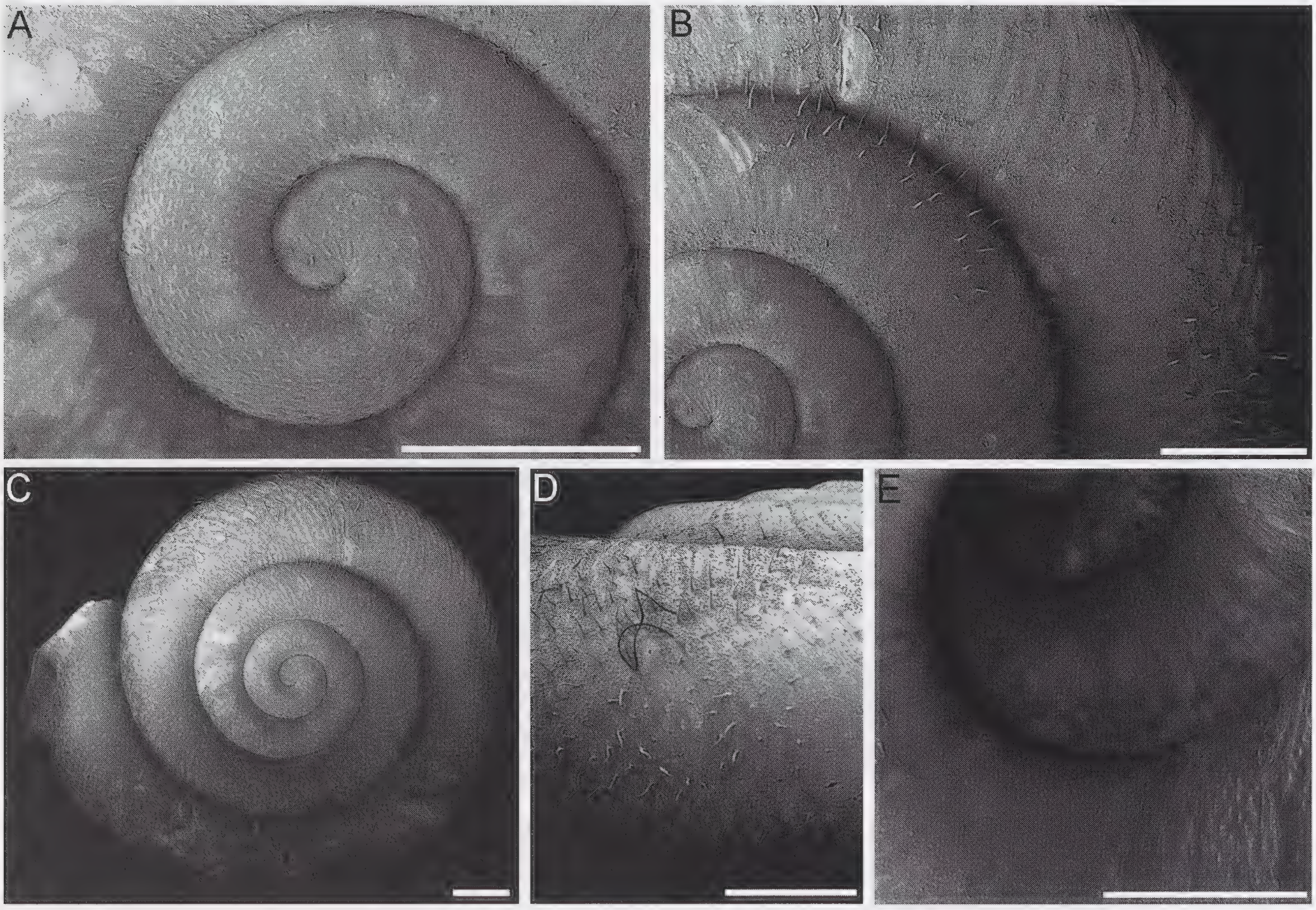

FIG. 157. SEM micrographs of the shell of ***Setobaudinia karczewski*** n. sp. paratype WAM S37887 (Molema Island). A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above; C: Entire shell viewed from above; D: Lateral view of last whorl showing distribution of periostracal hairs across whorl surface; E: Umbilicus. Scale bars = 1 mm.

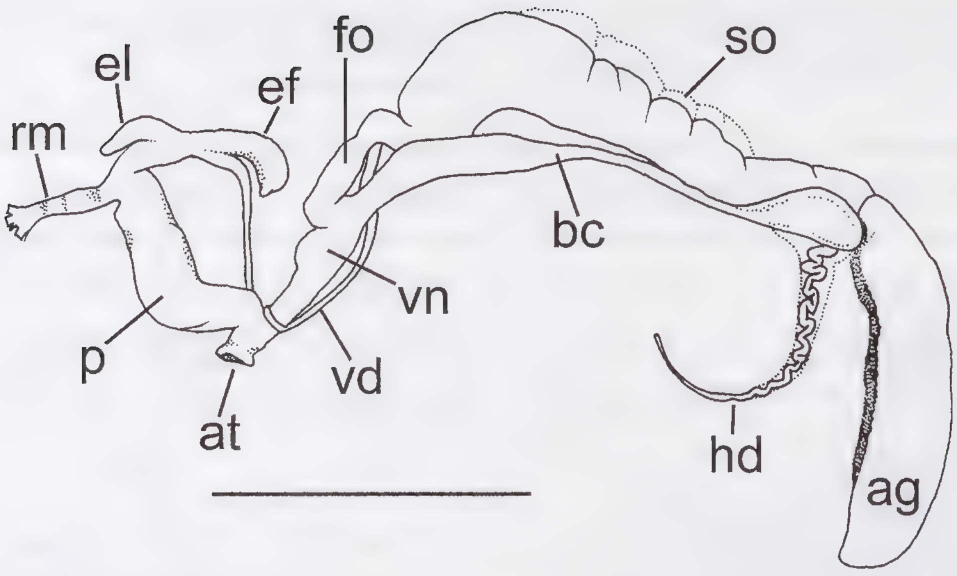

FIG. 158. Genital anatomy of **Setobaudinia karczewski** n. sp. holotype WAM S58482 (Molema Island, May). Scale bar = 5 mm.

with comparatively short epiphallic flagellum and epiphallic lobe; interiorly with one thick longitudinal epiphallic pilaster. Inner penial wall with well-developed, crowded, longitudinal pilasters comprising entire length of penial wall. Penial verge extending about half of penial chamber, thick, conical. Vagina tubular, elongate, about same length as free oviduct. Free oviduct comparatively long.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.008–0.025; interspecific genetic distances: 0.064–0.70 with respect to **S. joycei** (2 sequences), 0.155–0.180 to all congeners (30 sequences, 11 species).

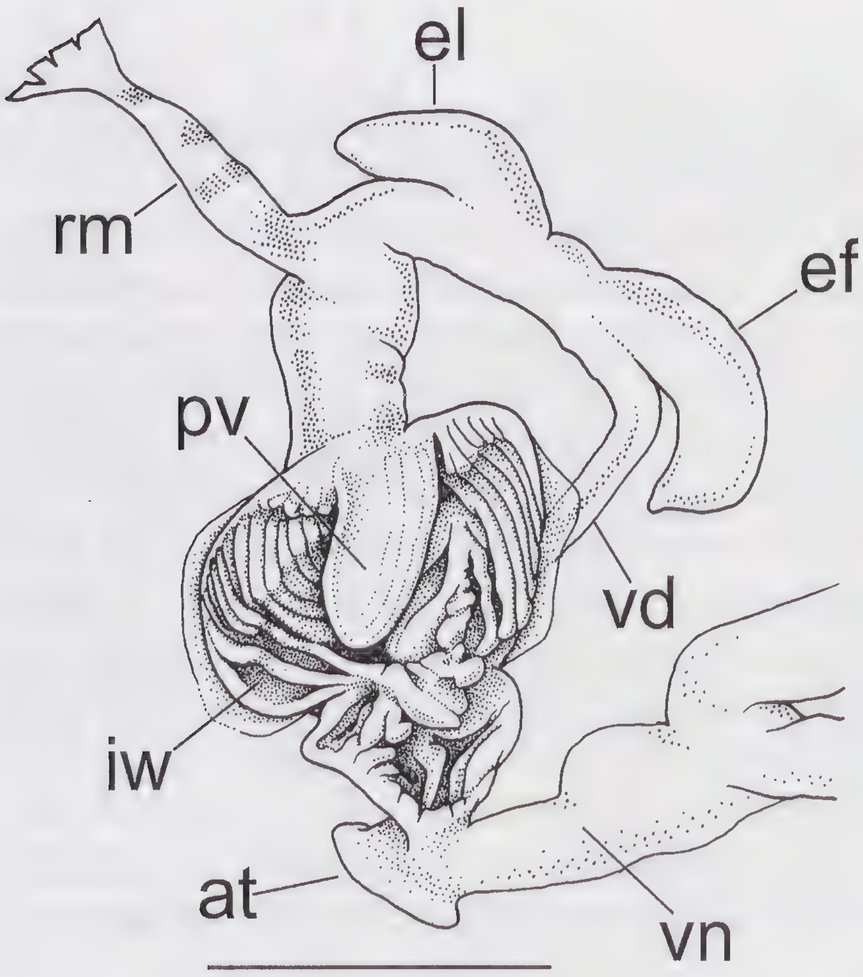

FIG. 159. Penial anatomy of **Setobaudinia karczewski** n. sp. holotype WAM S58482 (Molema Island, May). Scale bar = 2 mm.

Comparative Remarks

Inner penial wall sculpture consisting of many crowded longitudinal pilasters is most typical.

Distribution (Fig. 122)

Molema Island.

Torresitrachia Iredale, 1939

Torresitrachia Iredale, 1939: 48–49; Solem, 1979: 45–92; 1985a: 922–933 (partim), 1991: 178–185 (partim); Solem & McKenzie, 1991: 247–263 (partim); Willan et al., 2009: 87–102. Type species: *Helix endeauvourensis* Brazier, 1872, by original designation.

Taxonomic Remarks

Solem (1979) revised the nomenclatural history and pointed out that the taxon was validly described by Iredale (1939), although being mentioned earlier by Iredale (1933, 1938) as *nomen dubium*. The type species, *Helix endeauvourensis* is currently considered as junior synonym of *Helyx torresiana* Hombron & Jacquinot, 1841, from Cape York. Solem (1979) also demonstrated that general morphology of Western Australian species corresponds well with the type species from tropical Queensland. In addition, he listed *Magitrachia* Iredale, 1941 (type species *Planispira* (*Trachiopsis*) *blackiana* Preston, 1905, from Port Moresby, Papua New Guinea), as a synonym for its similar shell. Given rampant parallelism in the shell of Australian Camaenidae, I do not reiterate this suggestion but remark that the status of *Magitrachia* remains to be clarified.

Species exhibiting a penial anatomy that deviate from the diagnosis presented here are transferred to a new genus, ***Kimberleytrachia*** (see below). This treatment is well supported by molecular phylogenetic data (Köhler, 2009, 2010c) showing that both taxa form distinct clades that are not in a sister taxon relationship.

Diagnosis

Shell: Medium sized (D = 12–20 mm; Table 10), discoidal to broadly conical with sunken to slightly elevated spire, moderately increasing whorls separated by well-incised suture and

TABLE 10. Shell parameters of *Torresitrachia* (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Umbilicus (U)	Whorls	H/D Ratio
T. aquilonia n. sp.	HT	8.0	16.0	2.5	4.25	0.50
	17	7.2–8.5	14.5–16.6	2.4–2.9	4.0–4.3	0.46–0.53
		(7.8 ± 0.4)	(15.5 ± 0.6)	(2.6 ± 0.1)	(4.1 ± 0.1)	(0.50 ± 0.02)
T. eclipsis n. sp.	HT	8.8	15.6	2.7	4.4	0.56
	18	7.5–9.5	13.0–16.5	2.0–2.7	4.1–4.5	0.53–0.59
		(8.2 ± 0.6)	(14.6 ± 1.0)	(2.3 ± 0.2)	(4.3 ± 0.2)	(0.56 ± 0.02)
T. janszi n. sp.	HT	10.0	19.2	2.8	4.6	0.52
	5	10.0–10.8	17.8–19.5	2.6–3.1	4.1–4.7	0.52–0.59
		(10.3 ± 0.3)	(18.7 ± 0.7)	(2.9 ± 0.2)	(4.5 ± 0.2)	(0.55 ± 0.02)
T. urvillei n. sp.	HT	9.5	15.3	1.8	4.3	0.62
	17	7.3–10.0	12.7–17.6	1.5–2.2	3.8–4.7	0.55–0.64
		(8.7 ± 0.7)	(15.0 ± 1.2)	(2.0 ± 0.2)	(4.3 ± 0.2)	(0.58 ± 0.02)
T. brookei n. sp.	HT	7.7	13.8	1.7	4.1	0.56
	10	7.1–9.6	12.2–17.3	1.5–2.5	4.1–4.3	0.53–0.61
		(8.0 ± 0.6)	(14.2 ± 1.4)	(1.9 ± 0.3)	(4.2 ± 0.1)	(0.56 ± 0.02)
T. allouarni n. sp	HT	7.2	14.5	2.9	4.3	0.50
	12	6.4–8.1	13.8–16.3	2.5–3.0	4.2–4.7	0.40–0.52
		(7.1 ± 0.4)	(14.7 ± 0.7)	(2.7 ± 0.2)	(4.3 ± 0.1)	(0.48 ± 0.03)
T. flindersi n. sp	HT	7.1	14.5	2.7	4.25	0.49
	13	5.8–7.1	12.8–15.7	2.2–3.0	3.8–4.3	0.43–0.50
		(6.6 ± 0.4)	(14.4 ± 0.8)	(2.7 ± 0.2)	(4.1 ± 0.1)	(0.46 ± 0.02)
T. baudini n. sp.	HT	7.5	16.0	3.0	4.4	0.47
	19	7.1–9.0	14.8–17.5	2.5–3.2	4.3–4.7	0.46–0.54
		(8.0 ± 0.5)	(15.9 ± 0.6)	(2.8 ± 0.2)	(4.5 ± 0.1)	(0.51 ± 0.02)
T. tasmani n. sp.	HT	9.2	17	3.1	4.6	0.54
	15	8.0–9.8	15.9–19.0	2.5–3.5	4.4–4.8	0.48–0.54
		(8.8 ± 0.5)	(17.2 ± 0.9)	(3.1 ± 0.3)	(4.6 ± 0.1)	(0.50 ± 0.02)
T. freycineti n. sp.	HT	6.7	15	3.0	4.3	0.45
	19	5.5–8.0	12.0–16.5	2.5–3.6	4.0–4.5	0.44–0.53
		(6.9 ± 0.6)	(14.8 ± 1.1)	(2.9 ± 0.3)	(4.3 ± 0.2)	(0.47 ± 0.02)
T. houtmani houtmani n. sp.	HT	8.5	15.8	2.6	4.0	0.54
	20	7.2–10.5	13.9–18.0	1.8–3.0	3.8–4.7	0.52–0.62
		(9.4 ± 0.7)	(16.4 ± 1.0)	(2.3 ± 0.3)	(4.3 ± 0.2)	(0.57 ± 0.03)
T. houtmani dampieri n. sp.	HT	9.0	16.4	2.6	4.5	0.55
	26	8.4–10.6	15.8–18.8	2.3–3.0	4.1–4.7	0.51–0.62
		(9.6 ± 0.6)	(17.5 ± 0.8)	(2.6 ± 0.2)	(4.4 ± 0.2)	(0.55 ± 0.03)
T. leichhardti n. sp.	HT	7.0	14.6	2.7	4.1	0.48
	19	5.9–7.7	12.1–15.4	2.0–3.0	3.8–4.7	0.45–0.52
		(6.9 ± 0.5)	(14.1 ± 0.9)	(2.5 ± 0.3)	(4.2 ± 0.2)	(0.49 ± 0.02)
T. hartogi n. sp.	HT	8.5	17.9	3.1	4.3	0.47
	11	8.0–9.5	16.2–18.5	2.4–3.2	4.3–4.7	0.47–0.56
		(8.8 ± 0.4)	(17.3 ± 0.7)	(2.9 ± 0.2)	(4.5 ± 0.1)	(0.51 ± 0.03)
T. girgarinae n. sp.	3	6.3–7.1	13.1–14.2	2.0–2.7	3.8–4.1	0.48–0.51
		(6.7 ± 0.3)	(13.5 ± 0.5)	(2.4 ± 0.3)	(4.0 ± 0.1)	(0.50 ± 0.01)

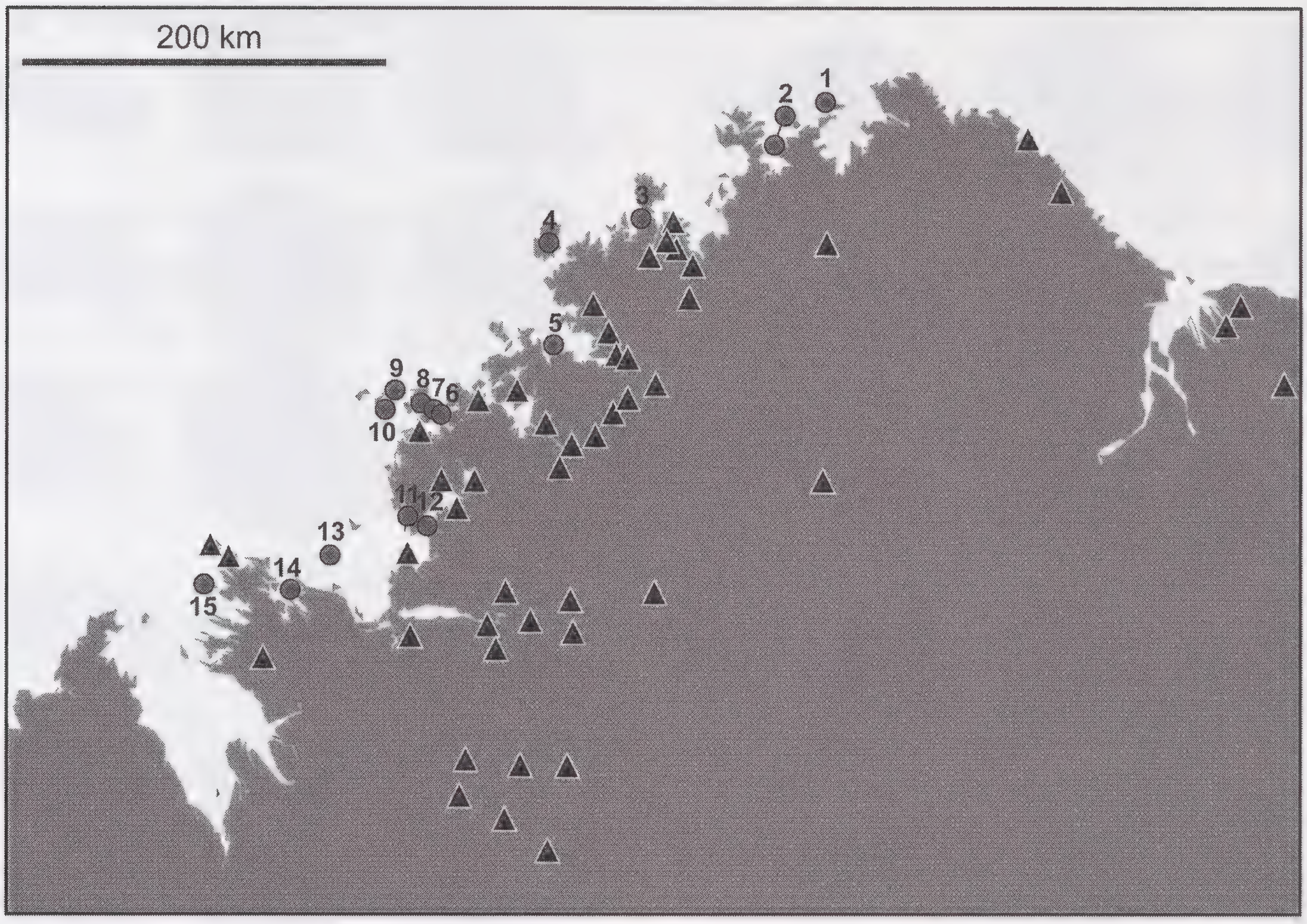

FIG. 160. Distribution map of *Torresitrachia* in the Kimberley. Circles = records of species treated herein: 1: ***T. aquilonia*** n. sp. (Sir Graham Moore Island), 2: ***T. eclipsis*** n. sp. (Eclipse Archipelago, Long and Jar Islands), 3: ***T. janszi*** n. sp. (Katers Island), 4: ***T. urvillei*** n. sp. (Bigge Island), 5: ***T. brookei*** n. sp. (Boongaree Island), 6: ***T. baudini*** n. sp. (unnamed islet SE of Augustus Island), 7: ***T. allouarni*** n. sp. (SE Augustus Island), 8: ***T. flindersi*** n. sp. (NW Augustus Island), 9: ***T. freycineti*** n. sp. (D'Arcy Island), 10: ***T. tasmani*** n. sp. (Byam Martin Island), 11: ***T. houtmani houtmani*** n. sp. & n. subsp. (unnamed island, Doubtful Bay), 12: ***T. leichhardti*** n. sp. (Storr Island), 13: ***T. houtmani dampieri*** n. subsp. (Kingfisher Island), 14: ***T. hartogi*** n. sp. (Molema Island), 15: ***T. girgarinae*** n. sp. (Hidden Island); triangles = records of various species listed by Solem (1979, 1985, 1991).

well-rounded periphery; umbilicus moderately open to nearly closed, partly concealed; protoconch with very weak to strongly developed, radially elongated pustulation; teleoconch mostly with well-developed axial ribs, usually extending onto base of shell but not into umbilicus; in some species with periostracal hairs or spines, and more or less developed pustulose microsculpture consisting of vertical, angled or spiral ridglets (frequently restricted to subsutural part of whorls), umbilical walls sparsely to densely covered by periostracal pustulation. Shell colour uniform, yellowish brown to brown. Last whorl not or weakly descending behind aperture; angle of aperture ~ 60°. Aperture slightly to strongly deflected from axis of coiling, partly covering umbilicus, with simple to slightly protruded basal lip and very thin parietal callus.

Genital anatomy: Penis without penial sheath, embedded in connective tissue; epiphallus well developed, with short to well-developed epiphallic flagellum. Inner penial wall with strongly developed, rhomboid pustules distally and longitudinal pilasters proximally. Penial retractor muscle attached at mid-portion of epiphallus. Epiphallus opens to penial lumen through constricting vergic ring. Inner epiphallic wall with longitudinal pilasters that vary in number and development, pustulation occasionally present; vas deferens opens through slit-like, valvular opening into epiphallus. Bursa copulatrix elongate, tubular, extending to anterior end of albumen gland.

Aestivation Strategy

Free sealer (modified after Solem, 1985a).

Comparative Remarks

Torresitrachia is characterized by combination of rather small to moderate shell size, discoidal to broadly conical shape, regular and conspicuous ribbing (only exceptionally ribs are weak and well-developed hairs are present, such as in *Torresitrachia alenae* Willan, Köhler; Kessner & Braby, 2009) and a narrowly winding, essentially unconcealed umbilicus. Typical combination of genital characters are: lack of penial sheath, presence of well-developed epiphallus with flagellum, separation of epiphallic and penial lumen by constricting, circular vergic ring, tubular bursa copulatrix extending until anterior end of albumen gland, inner penial wall with pustulation distally and longitudinal pilasters proximally. Species previously affiliated with *Torresitrachia* that differ from this typical anatomy by having relatively large but delicate shells with pustulose microsculpture, a strongly descending last whorl (rock sealers) and formation of lateral lamellae at distal end of inner penial wall (instead of rhomboid pustules) form a distinct, monophyletic group and are transferred to the new genus ***Kimberleytrachia*** described below. Due to conserved shell morphology, most *Torresitrachia* species are distinguishable by their genital anatomy only.

Diversity and Distribution (Fig. 160)

Torresitrachia ranges across the tropical north of Australia from the Torres Strait, northern Queensland in the east to the southwest Kimberley in the west, although currently no species are known from the Gulf of Carpentaria area. As delimited by Solem (1979) to include as *Magitrachia* Iredale, 1941, a junior synonym, the taxon also occurs in Papua New Guinea. However, this assumption requires confirmation by comparative study of suitable material from that region. The highest diversity is found in western parts of the range with six out of eleven previously known species occurring in the Kimberley plus four in northern parts of the Northern Territory, between Kununurra and Katherine (this does not include species herein assigned to ***Kimberleytrachia***, n. gen.). Only one species is currently recognized from Cape York. Herein, 15 species are newly described, all of which are narrowly endemic to an island or even only parts of islands. Based on observation that shell morphology of most species is rather conserved and that species ranges are usually small, I predict that there is a high proportion of undiscovered species across the entire range of the genus.

Torresitrachia aquilonia n. sp.

Figs. 161A, 162–164

Type Locality

Western Australia, northern Kimberley, Eclipse Archipelago, eastern section of Sir Graham Moore Island, 13°53'51"S, 126°35'53"E; coll. Vince Kessner, 9/08/2007, KIS 3–40 (patches of vine thicket on dunes, under logs in loose soil).

Material Examined

Holotype. WAM S58451 (preserved specimen, Fig. 161A). Paratypes AM C471757 (20 preserved specimens), WAM S36632 (29 preserved specimens), AM C471758 (20 shells), WAM S36438 (47 shells) from type locality; WAM S36633 (16 preserved specimens), WAM S36565 (10 shells) from 13°54'05"S, 126°35'51"E; WAM S36631 (13 preserved specimens), WAM S36437 (2 shells) from 13°53'56"S, 126°35'59"E; WAM S36452 (16 shells) from 13°54'14"S, 126°36'01"E; WAM S36959 (20 shells) from 13°53'50"S, 126°35'51"E; AM C471759 (10 shells), WAM S36960 (20 shells) from 13°54'06.2"S, 126°35'53.4"E.

Etymology

From "*aquilonia*" (Latin = northern), for being the northernmost species of *Torresitrachia* currently known from the Kimberley, adjective of feminine gender.

Description

Shell (Figs. 161A, 162A–D): Moderate in size (D = 14.5–16.6 mm; Table 10), nearly discoidal with low spire; umbilicus ~ 2.5 mm wide; colour light brownish-horn, with glossy surface. Protoconch ~ 2.3 mm in diameter, comprising about 1.5 whorls, essentially smooth. Teleoconch with regularly and narrowly spaced radial ribs; inner umbilical whorls with microsculpture of fine periostracal extensions. Apertural lip sharp, well- to strongly expanded, slightly reflected, well rounded, without nodes, parietal wall extremely delicate.

Digestive anatomy (Fig. 162E–G): Jaw consisting of many plates. Radula 4 mm long, with about 150 rows of teeth; C + 13–14 + 2–3 + 18–20 (n = 1).

Genital anatomy (Figs. 163–164): Penis shorter than vagina, bent or coiled. Epiphallus coiled, almost as long as penis, with short

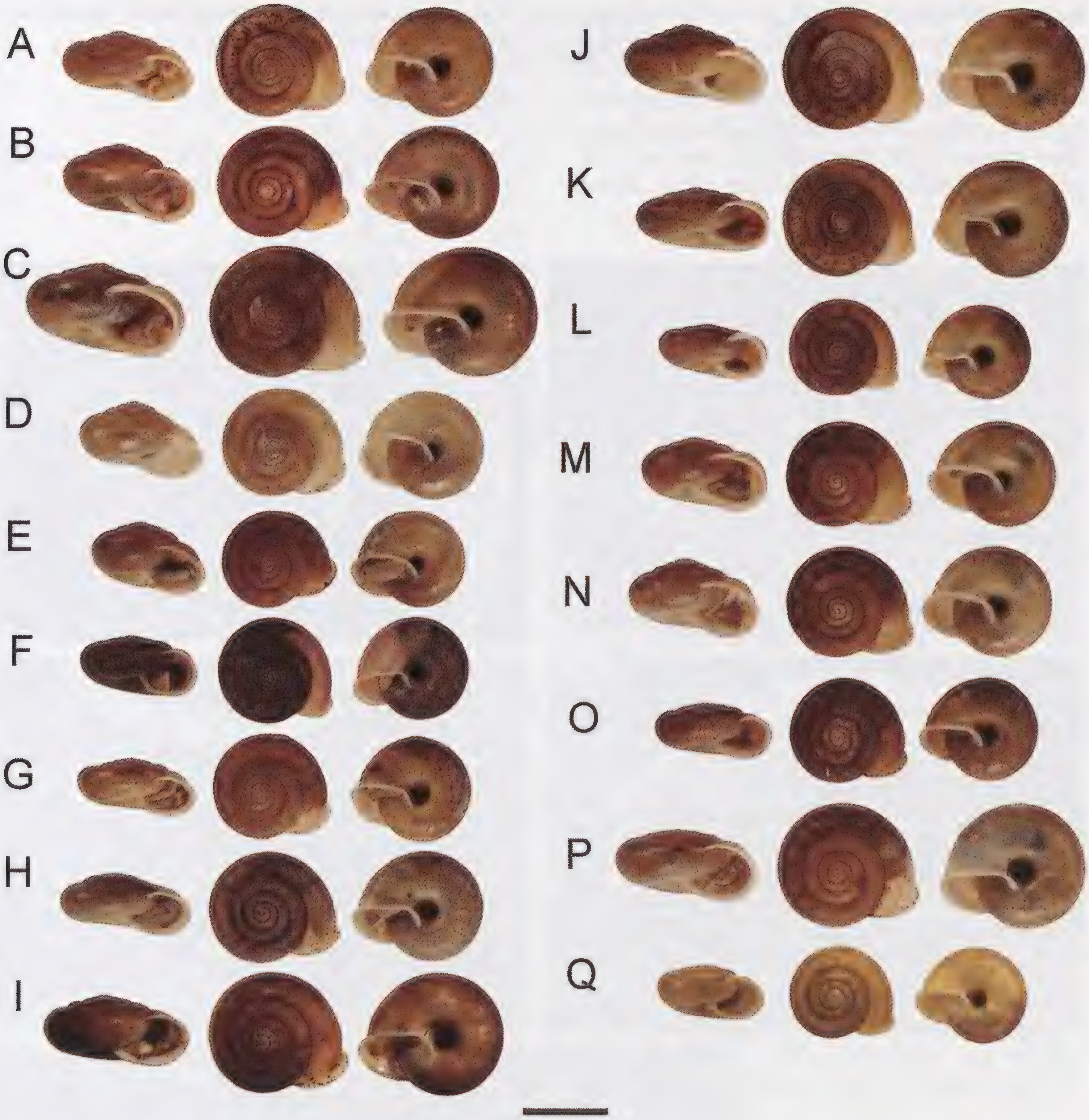

FIG. 161. Shells of *Torresitrachia* species. A: ***Torresitrachia aquilonia*** n. sp. holotype WAM S58451 (Sir Graham Moore Island); B: ***Torresitrachia eclipsis*** n. sp. holotype WAM S58452 (Long Island, Eclipse Archipelago); C: ***Torresitrachia janszi*** n. sp. paratype WAM S36626 (Katers Island); D: ***Torresitrachia urvillei*** n. sp. holotype WAM S58454 (Bigge Island); E: ***Torresitrachia brookei*** n. sp. holotype WAM S36735 (Boongaree Island); F: ***Torresitrachia allouarni*** n. sp. holotype WAM S58455 (Augustus Island, SE section); G: ***Torresitrachia flindersi*** n. sp. holotype WAM S58456 (Augustus Island, NW section); H: ***T. flindersi*** n. sp. paratype WAM S37648 (Augustus Island, NW section); I: ***Torresitrachia baudini*** n. sp. holotype WAM S58457 (Islet SE of Augustus Island); J: ***Torresitrachia tasmani*** n. sp. holotype WAM S58458 (Byam Martin Island); K: ***Torresitrachia freycineti*** n. sp. paratype WAM S37645 (D'Arcy Island); L: ***T. freycineti*** n. sp. paratype WAM S37018 (D'Arcy Island); M: ***Torresitrachia houtmani houtmani*** n. sp. & n. subsp. holotype WAM S58463 (unnamed island, Doubtful Bay); N: ***T. houtmani dampieri*** n. subsp. holotype WAM S58462 (Kingfisher Island); O: ***Torresitrachia leichhardti*** n. sp. holotype WAM S58460 (Storr Island); P: ***Torresitrachia hartogi*** n. sp. holotype WAM S58461 (Molema Island); Q: ***Torresitrachia girgarinae*** n. sp. paratype WAM S37871 (Hidden Island). Scale bar = 10 mm. Note that foot produces from some shells.

epiphallic flagellum. Distal third of inner penial wall with comparatively small, densely packed, roundish pustules, proximal two thirds with indistinct longitudinal pilasters. Penial retractor muscle shorter than epiphallus. Vagina longer than free oviduct, tubular, inner wall with longitudinal pilasters. Free oviduct short, coiled. Bursa copulatrix with inflated head, extending the anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.0; interspecific genetic distances: 0.131–

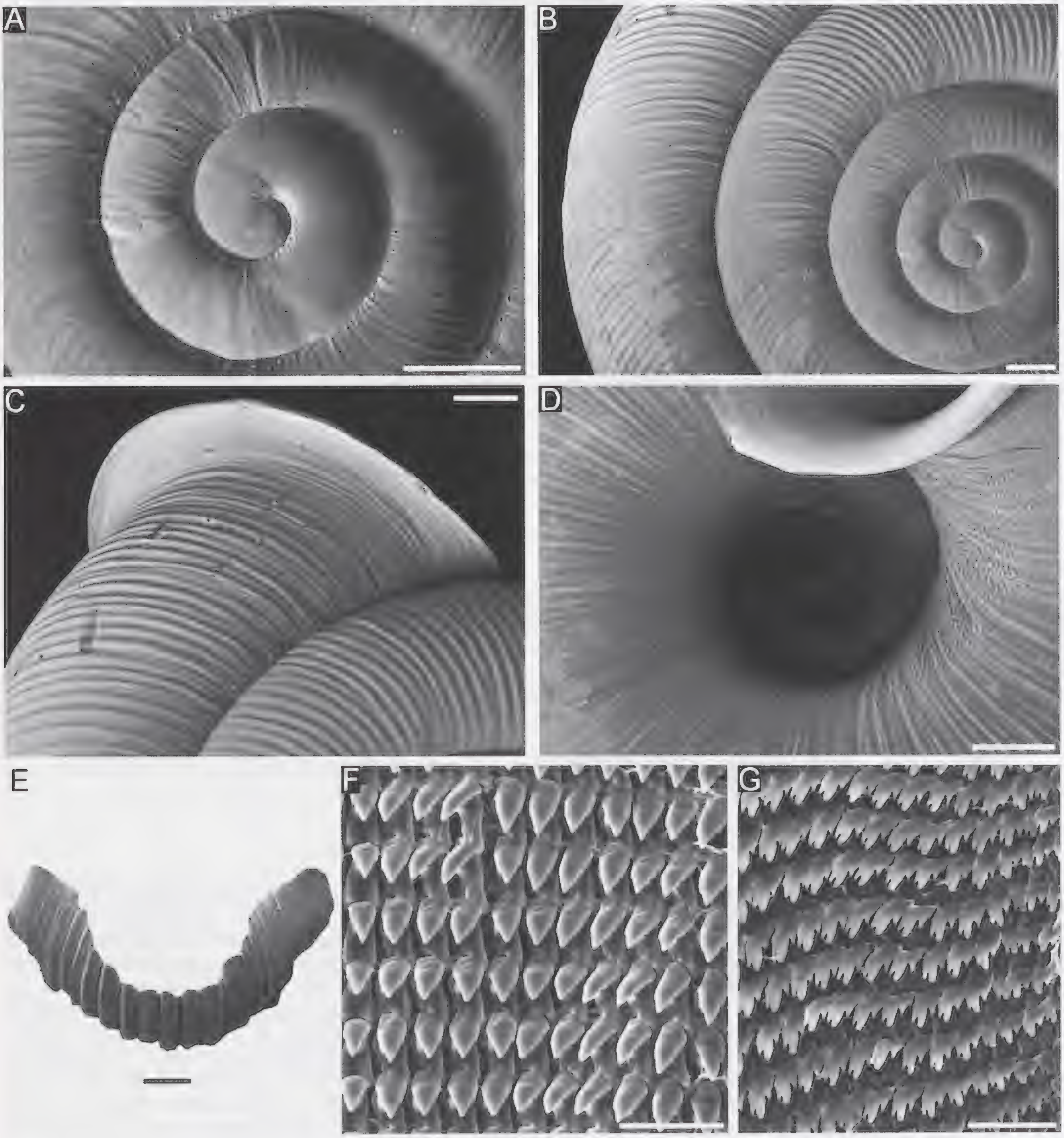

FIG. 162. SEM micrographs of ***Torresitrachia aquilonia*** n. sp. (Sir Graham Moore Island). A–D: Shell paratype AM C471759. Scale bars = 1 mm. A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl near apertural lip viewed from above; D: Umbilicus; E: Jaw paratype AM C471757. Scale bar = 200 µm; F–G: Radula paratype AM C471757. Scale bars = 50 µm; F: Central and lateral teeth viewed from above; G: Middle marginal teeth viewed from above.

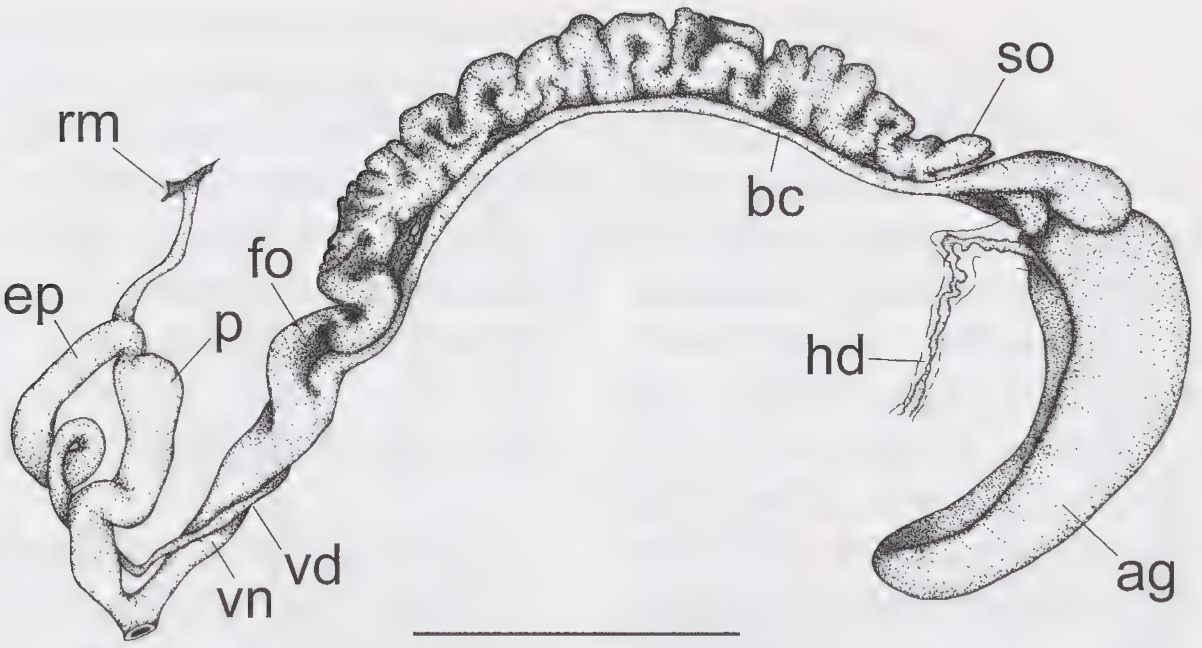

FIG. 163. Genital anatomy of ***Torresitrachia aquilonia*** n. sp. paratype AM C471757 (Sir Graham Moore Island, August). Scale bar = 5 mm.

0.161 with respect to ***T. allouarni***, ***T. baudini***, ***T. flindersi***, ***T. freycineti***, ***T. girgarinae***, ***T. hartogi***, ***T. leichhardti***, and ***T. tasmani***; 0.231–0.236 to all other congeners.

Comparative Remarks

Typical are an inflated head of bursa copulatrix extending the anterior end of albumen gland and penial wall with small crowded pustules at distal third and broad but indistinct longitudinal pilasters at proximal two thirds. Penial wall sculpture of ***T. brookei*** is similar (see below).

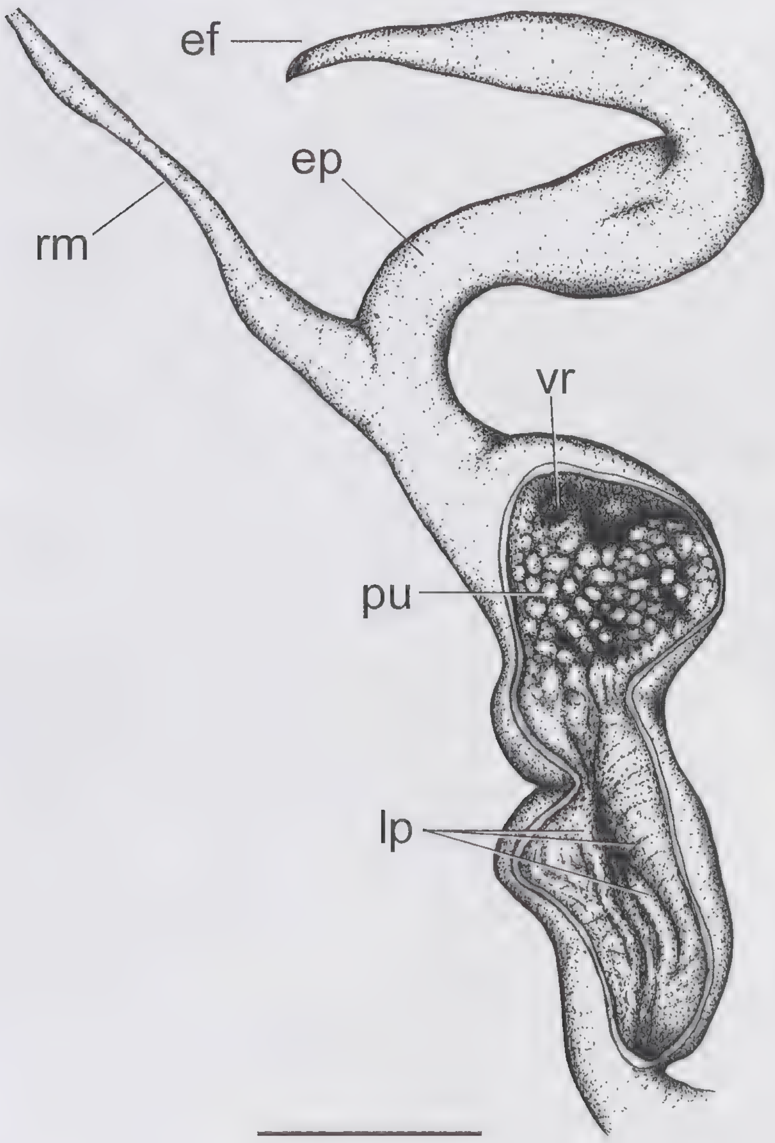

FIG. 164. Penial anatomy of ***Torresitrachia aquilonia*** n. sp. paratype AM C471757 (Sir Graham Moore Island, August). Scale bar = 1 mm.

Distribution (Fig. 160)

Sir Graham Moore Island.

Torresitrachia eclipsis n. sp.

Figs. 161B, 165–167

Type Locality

Western Australia, northern Kimberley Vansittart Bay, Eclipse Archipelago, Long Island, 13°56'04"S, 126°18'26"E; coll. Vince Kessner, 4/06/2010, KIS 3–199 (coastal vine thicket patches on dunes and laterite; common, buried in sand).

Material Examined

Holotype WAM S58452 (preserved specimen). Paratypes WAM S49356 (preserved specimens), AM C471760 (40 shells), WAM S49348 (68 shells) from type locality.

Additional, non-type material. WAM S49347 (2 shells) from Jar Island, 14°08'59"S, 126°14'10"E.

Etymology

From "*eclipsis*" (Latin = eclipse), in reference to Eclipse Islands, where this species occurs; noun in apposition.

Description

Shell (Figs. 161B, 165): Moderate in size (D = 13.0–16.5 mm; Table 10), very broadly conical with moderately elevated spire; periphery well rounded to slightly depressed; umbilicus ~ 2.3 mm wide; glossy surface. Protoconch ~ 2.3 mm in diameter, comprising about one whorl, essentially smooth. Teleoconch with regularly and narrowly spaced radial ribs; inner umbilical whorls with microsculpture of fine periostracal extensions. Apertural lip sharp, weakly expanded, slightly reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 166–167): Penis as long as vagina, straight. Epiphallus coiled, clearly shorter than penis, with moderately long epiphallic flagellum. Distal three quarters of inner penial wall with large, rhomboid pustules, densely arranged in honeycomb pattern; pad-like elevated underneath opening to epiphallus; proximal end with five to six short, well-defined longitudinal pilasters. Inner epiphallic wall with longitudinal pilasters. Penial retractor muscle short. Vagina longer than free oviduct, slightly inflated. Free oviduct short, coiled. Bursa copulatrix with slightly inflated head, barely reaching anterior end of albumen gland.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.143–0.160 with respect to ***T. brookei***, ***T. urvillei***, *T. dampieri*, and ***T. janszi***; 0.194–0.226 to all other congeners.

Comparative Remarks

Shell more elevated than in ***T. aquilonia***, with narrower umbilicus, last whorl slightly depressed rather than slightly shouldered above periphery, apertural lip not as strongly expanded, surface not as glossy. Penial wall

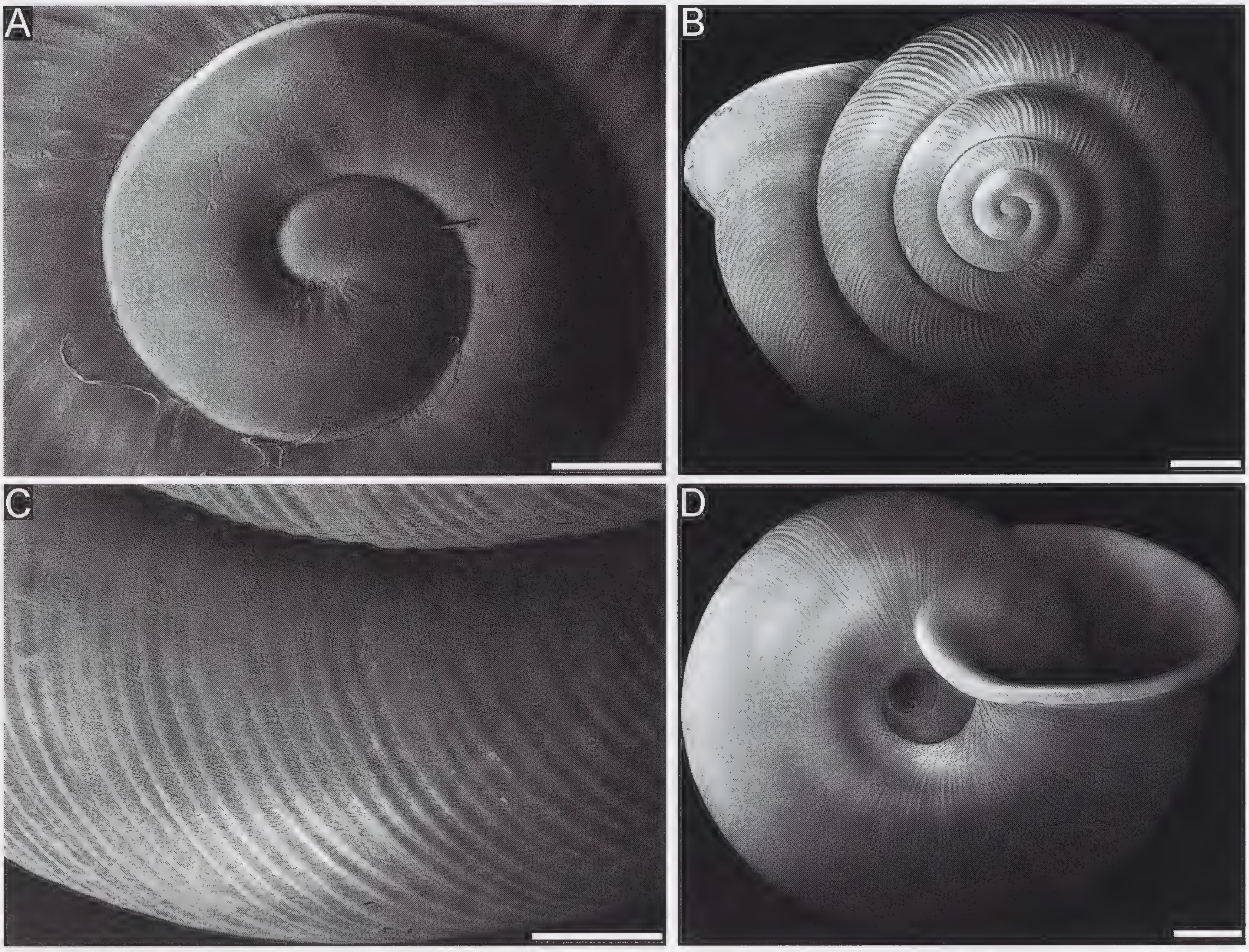

FIG. 165. SEM micrographs of the shell of ***Torresitrachia eclipsis*** n. sp. paratype AM C471760 (Long Island, Vansittart Bay). A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across entire shell viewed from above. Scale bar = 2 mm; C: Close-up of sculpture on last whorl viewed from above. Scale bar = 1 mm; D: Shell viewed from below showing umbilicus and aperture. Scale bar = 2 mm.

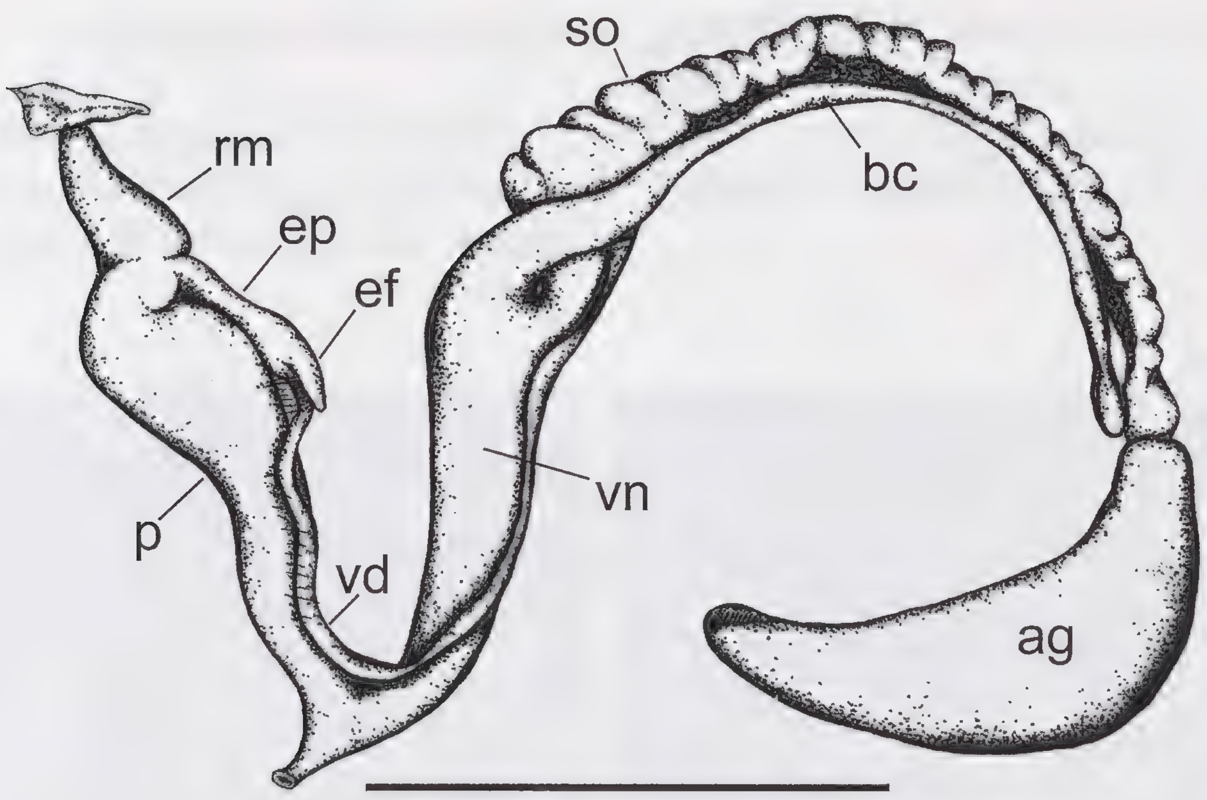

FIG. 166. Genital anatomy of ***Torresitrachia eclipsis*** n. sp. paratype WAM S49346 (Long Island, Vansittart Bay, June). Scale bar = 5 mm.

sculpture is typical for this species; only ***T. janszi*** being similar (see below).

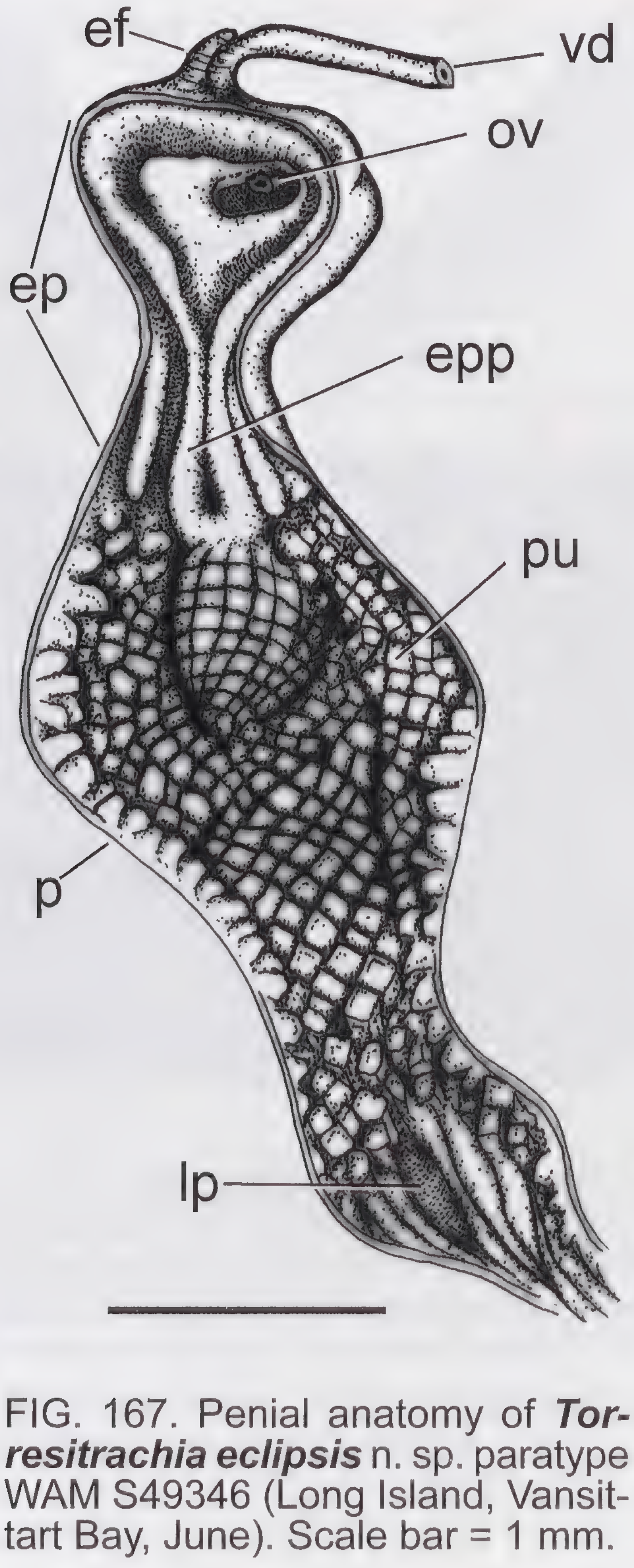

FIG. 167. Penial anatomy of ***Torresitrachia eclipsis*** n. sp. paratype WAM S49346 (Long Island, Vansittart Bay, June). Scale bar = 1 mm.

Distribution (Fig. 160)

Long and Jar islands, Vansittart Bay, Eclipse Archipelago.

Torresitrachia amaxensis
Solem, 1979

Torresitrachia amaxensis Solem, 1979: 79–84, pls 4e–f, 5g–l, figs. 15a–c, 16a, b; 1985a: 923, 1991: 181.

Type Locality

Camp Creek, Mitchell Plateau.

Taxonomic Remarks

The name was introduced for specimens from several localities in the Mitchell Plateau. Solem (1985a) reported shells from Bigge Island, while Solem (1991) stated that affinities of specimens from Katers and Bigge Island remain doubtful. During the Kimberley Survey this species was not found on these islands but yet undescribed species were found. *Torresitrachia amaxensis* is probably restricted to the Mitchell Plateau and is unlikely to occur on off-shore islands.

Diagnosis

Shell: Comparatively large (D = 18–20 mm), broadly conical with elevated spire; umbilicus ~ 1.5 mm wide. Regularly and narrowly spaced radial ribs nearly absent from base of shell.

Genital anatomy: Penis comparatively large in size, with inflated posterior portion. Distal half of inner penial wall with crowded, rhomboid pustules with hooked tip, proximal portion with well-developed longitudinal pilasters. Inner epiphallic wall with thick longitudinal pilasters (after Solem, 1979).

Comparative Remarks

Typical features of penial wall sculpture are crowded, large, rhomboid, hooked pustules at distal half of interior wall and crowded, strongly

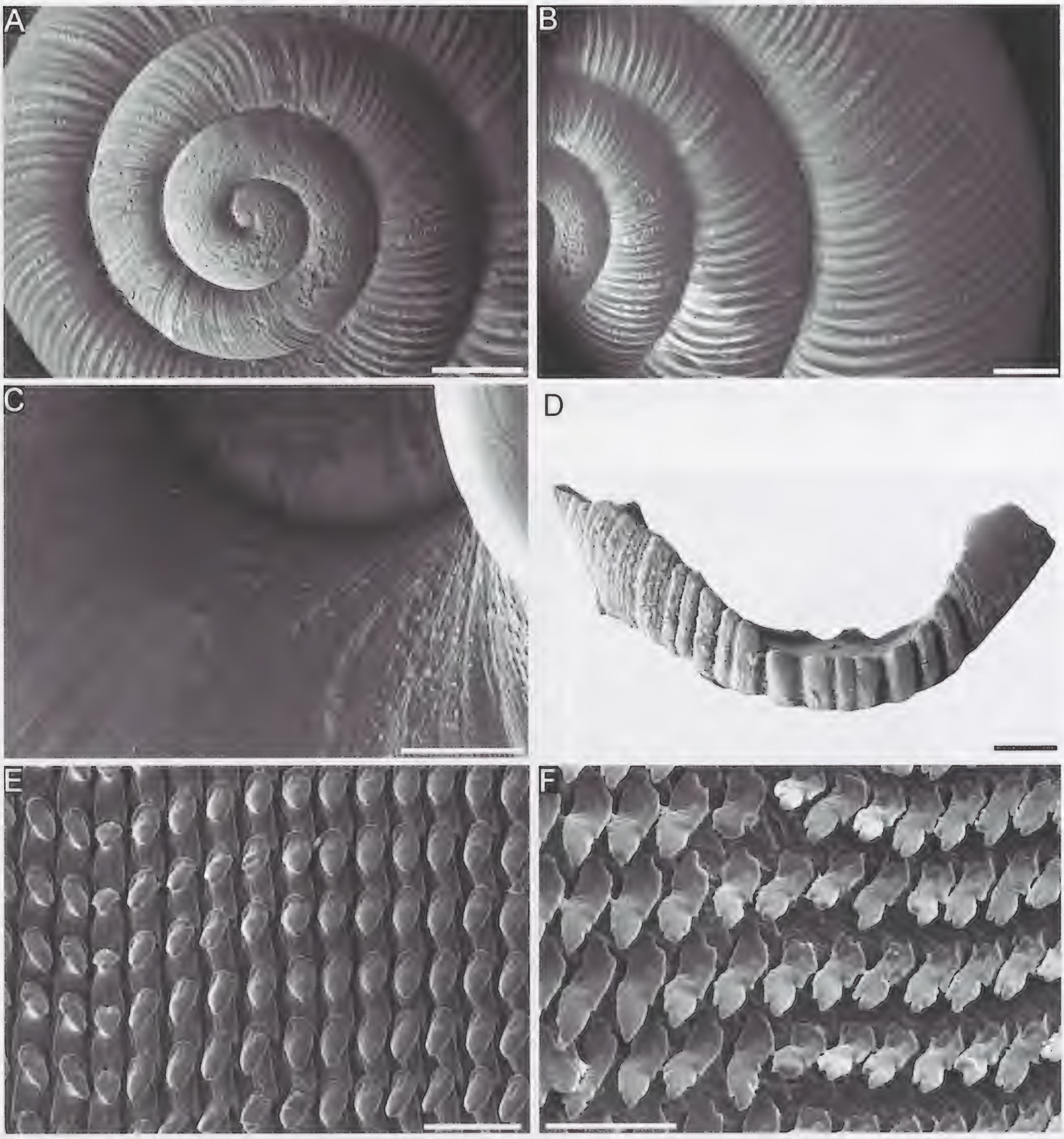

FIG. 168. SEM micrographs of ***Torresitrachia janszi*** n. sp. (Katers Island). A–C: Shell paratype AM C471762. Scale bars = 1 mm. A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of inner umbilical whorls showing periostracal granules; D: Jaw holotype WAM S58453. Scale bar = 200 µm; E–F: Radula holotype WAM S58453. Scale bars = 50 µm; E: Central and lateral teeth viewed from above; F: Transitional and middle marginal teeth viewed from above.

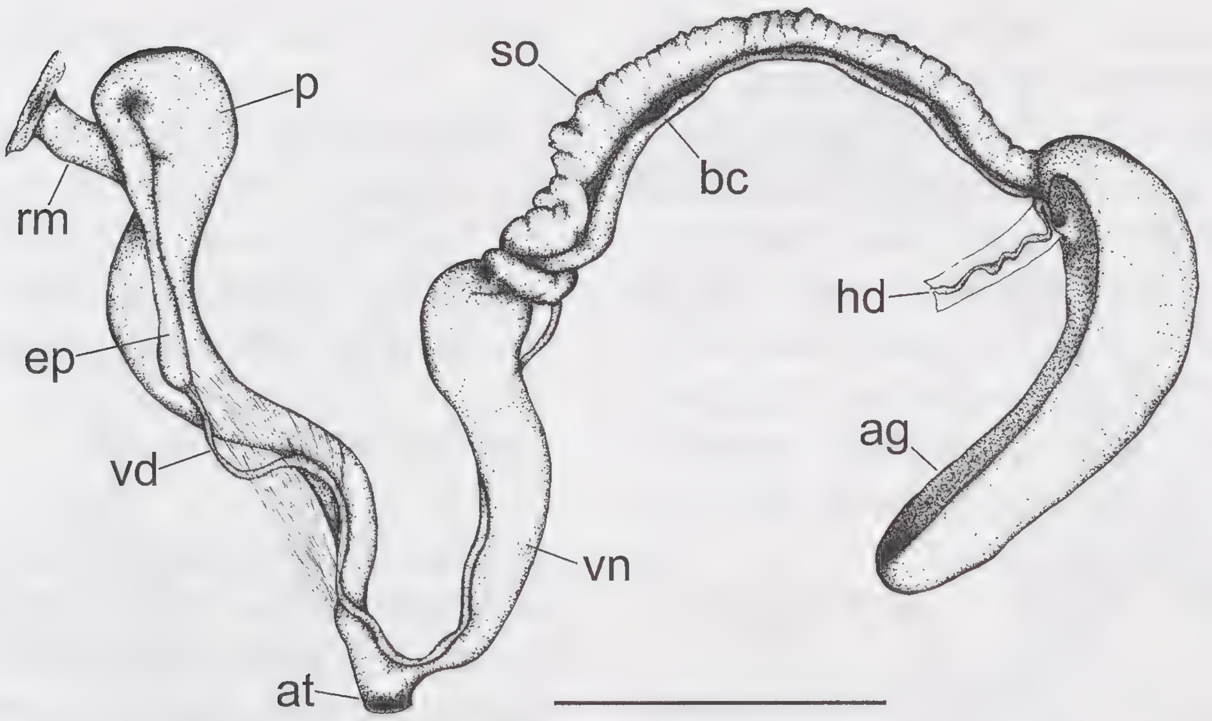

FIG. 169. Genital anatomy of ***Torresitrachia janszi*** n. sp. holotype WAM S58453 (Katers Island, July). Scale bar = 3 mm.

developed longitudinal pilasters at proximal half, inflated distal proper of penis, comparatively short, inflated epiphallus. ***Torresitrachia aquilonia*** has fewer, smaller and roundish pustules and more indistinct pilasters.

Torresitrachia janszi n. sp.
Figs. 161C, 168–170

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Montague Sound, W section of Katers Island, 14°26’51.0”S, 125°30’51.7”E; coll. Roy Teale, 30/07/2007, KIS 2–6 (N-facing slope in woodland/vine thicket, dolerite derived soils, sandstone scree; under logs and rocks).

Material Examined

Holotype WAM S58453 (preserved specimen, dissected). Paratypes WAM S36628 (4 preserved specimens) from type locality; WAM S36626 (preserved specimen) from 14°26’51.6”S, 125°31’07.1”E; WAM S36627 (2 preserved specimens), WAM S36418 (shell) from 14°26’57.5”S, 125°31’08.7”E; WAM S36629 (preserved specimen), WAM S36419 (shell) from 14°26’45.6”S, 125°31’16.1”E; WAM S36420 (shell) from 14°26’32.4”S, 125°31’14.4”E; WAM S36870 (5 preserved specimens) from 14°26’52”S, 125°31’13”E; AM C471761 (2 preserved specimens), WAM S36871 (5 preserved specimens), AM C471762 (2 shells), WAM S36965 (4 shells) from 14°26’49”S, 125°31’15”E.

Etymology

In honour of Willem Jansz, the first European explorer to make authenticated discovery of Australia when in command of the *Duyfken* in 1606; noun in genitive case.

Description

Shell (Figs. 161C, 168A–C): Large (D = 17.8–19.5 mm; Table 10), broadly conical with moderately elevated spire; umbilicus ~ 3 mm

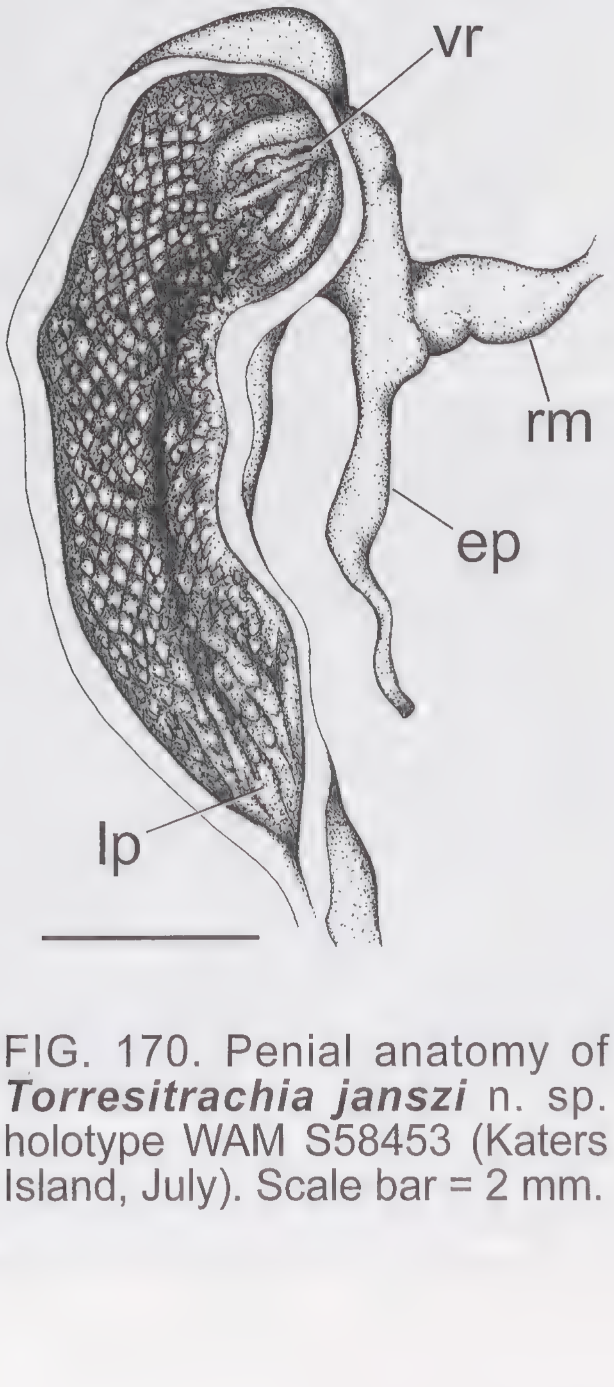

FIG. 170. Penial anatomy of ***Torresitrachia janszi*** n. sp. holotype WAM S58453 (Katers Island, July). Scale bar = 2 mm.

wide; colour horn, glossy. Protoconch ~ 2.3 mm in diameter, comprising about 1.5 whorls, essentially smooth with erosion scars. Teleoconch with fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls sculptured with microsculpture of fine periostracal pustules. Apertural lip sharp, well expanded, weakly reflected, well rounded without nodes, parietal wall extremely delicate.

Radula (Fig. 168D–F): C + 20 + 2–3 + ? (n = 1).

Genital anatomy (Figs. 169–170): Penis longer than vagina, straight. Epiphallus clearly shorter than penis, with tiny epiphallic flagellum. Distal three quarters of inner penial wall with small, rhomboid pustules, densely arranged in honeycomb pattern; proximal end with five to six short, well-defined longitudinal pilasters. Inner epiphallic wall with longitudinal pilasters. Penial retractor muscle short. Vagina longer than free oviduct, inflated. Free oviduct very short, coiled. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.0–0.003; interspecific genetic distances: 0.136–0.157 with respect to ***T. brookei***, *T. dampieri*, ***T. eclipsis***, and ***T. urvillei***; 0.211 to 0.236 to all other congeners.

Comparative Remarks

Shell larger than that of ***T. aquilonia*** and ***T. eclipsis***; unlike in the former two species ribs on shell do not extend into umbilicus. Typical feature of penial wall sculpture is presence of small, rhomboid pustules, densely arranged in honeycomb pattern comprising almost entire length of wall. ***Torresitrachia eclipsis*** differs by having larger pustules and much shorter penis relative to length of vagina. Number of lateral teeth of radula larger than in ***T. aquilonia***.

Distribution (Fig. 160)

Katers Island.

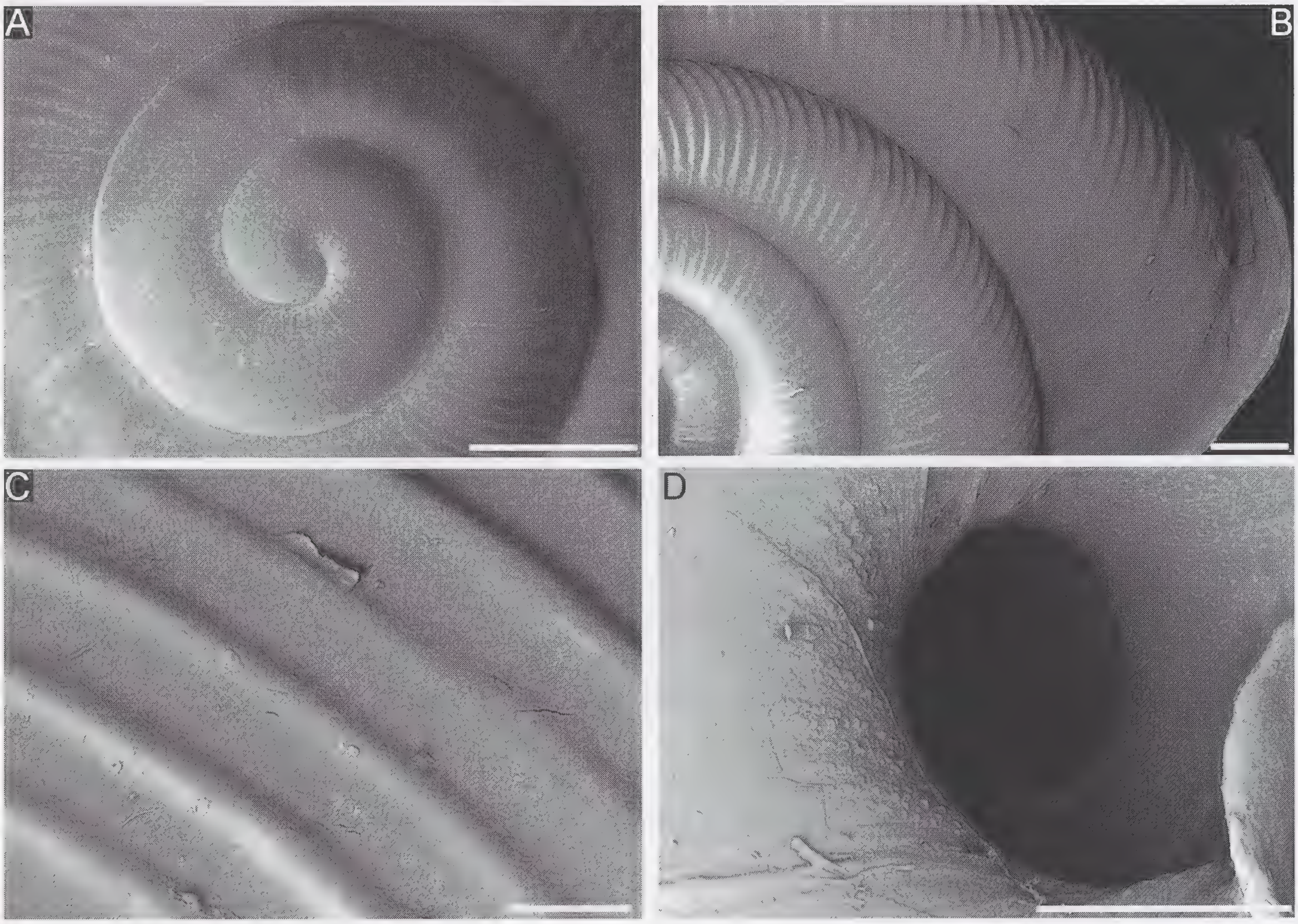

FIG. 171. SEM micrographs of the shell of ***Torresitrachia urvillei*** n. sp. paratype AM C471764 (Bigge Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl; D: Umbilicus. Scale bars A–B, D = 1 mm, C = 200 µm.

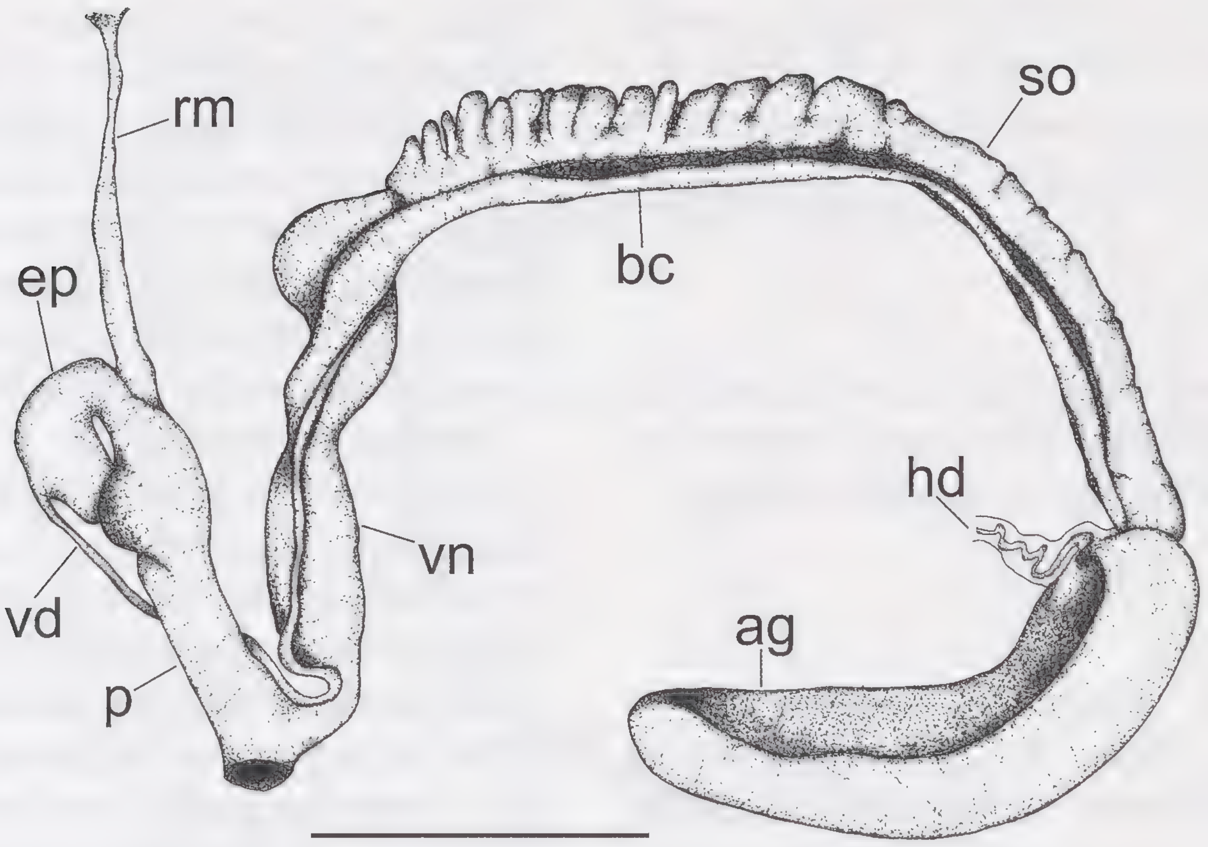

FIG. 172. Genital anatomy of ***Torresitrachia urvillei*** n. sp. paratype AM C471763 (Bigge Island, July). Scale bar = 3 mm.

Torresitrachia urvillei n. sp.

Figs. 161D, 171–173

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Bigge Island, 4.16 km NNE of Savage Hill, 14°35'19"S, 125°11'08"E; coll. Michael Shea, 29/07/2007, KIS 1–9 (dry vine thicket on creek floodplain; in rotting *Pandanus* logs).

Material Examined

Holotype WAM S58454 (preserved specimen, Fig. 161D). Paratypes AM C471763 (7 preserved specimens), WAM S36649 (11 preserved specimens), WAM S36427 (2 shells) from type locality; AM C471764 (5 shells), WAM S36421 (10 shells) from 14°35'20"S, 125°11'07"E; WAM S36730 (5 preserved specimens), WAM S36422 (2 shells) from 14°35'27"S, 125°11'03"E; WAM S36423 (shell) from 14°35'16"S, 125°11'06"E; WAM S36731 (3 preserved specimens), WAM S36424 (5 shells) from 14°35'33"S, 125°11'19"E; WAM S36425 (13 shells) from 14°35'14"S, 125°11'08"E; WAM S36426 (2 shells) from 14°35'14"S, 125°10'53"E; WAM S36428 (2 shells) from 14°35'10"S, 125°11'06"E; WAM S36429 (2 shells) from 14°34'35"S, 125°05'57"E; WAM S36430 (3 shells) from 14°35'06"S, 125°06'12"E; WAM S36453 (2 shells) from 14°35'16"S, 125°11'02"E; AM C471765 (6 shells), WAM S36453 (10 shells) from 14°34'59"S, 125°06'22"E; WAM S36732 (6 preserved specimens) from 14°35'06"S, 125°06'08"E; WAM S36733 (6 preserved specimens), WAM S36731 (2 shells) from 14°35'06"S,

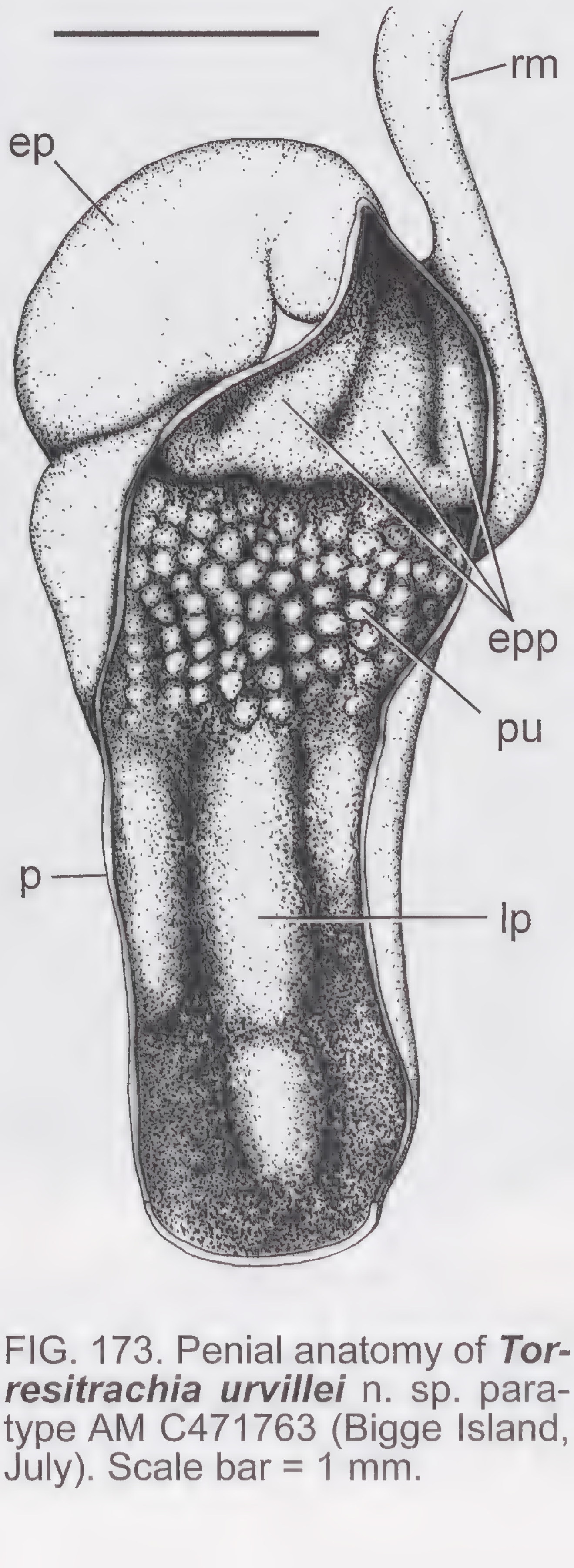

FIG. 173. Penial anatomy of ***Torresitrachia urvillei*** n. sp. paratype AM C471763 (Bigge Island, July). Scale bar = 1 mm.

125°06'12"E; WAM S36897 (3 preserved specimens) from 14°35'15"S, 125°11'05"E; WAM S36902 (4 preserved specimens) from 14°35'18.5"S, 125°10'54.7"E.

Etymology

In honour of Jules Dumont d'Urville, who in 1826 led an expedition to Western Australia on board the *Astrolabe*; noun in genitive case.

Description

Shell (Figs. 161D, 171): Moderate in size (D = 12.7–17.6 mm; Table 10), broadly conical with moderately elevated spire; periphery well rounded to slightly depressed, whorls separated by rather shallow suture; umbilicus ~ 2.2 mm wide; colour brownish horn, not glossy. Protoconch ~ 2.3 mm in diameter, comprising about one whorl, essentially smooth. Teleoconch with fine, regularly spaced radial ribs, becoming more indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls sculptured with microsculpture of fine periostracal pustules. Apertural lip sharp, rather weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 172–173): Penis moderately shorter than vagina, straight. Epiphallus shorter than penis, with small epiphallic flagellum. Distal third of inner penial wall with small, roundish pustules, densely arranged in honeycomb pattern; proximal two thirds with three broad, rather indistinct longitudinal pilasters. Inner epiphallic wall with four longitudinal pilasters. Penial retractor muscle longer than penis. Vagina longer than free oviduct, inflated. Free oviduct very short, coiled. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

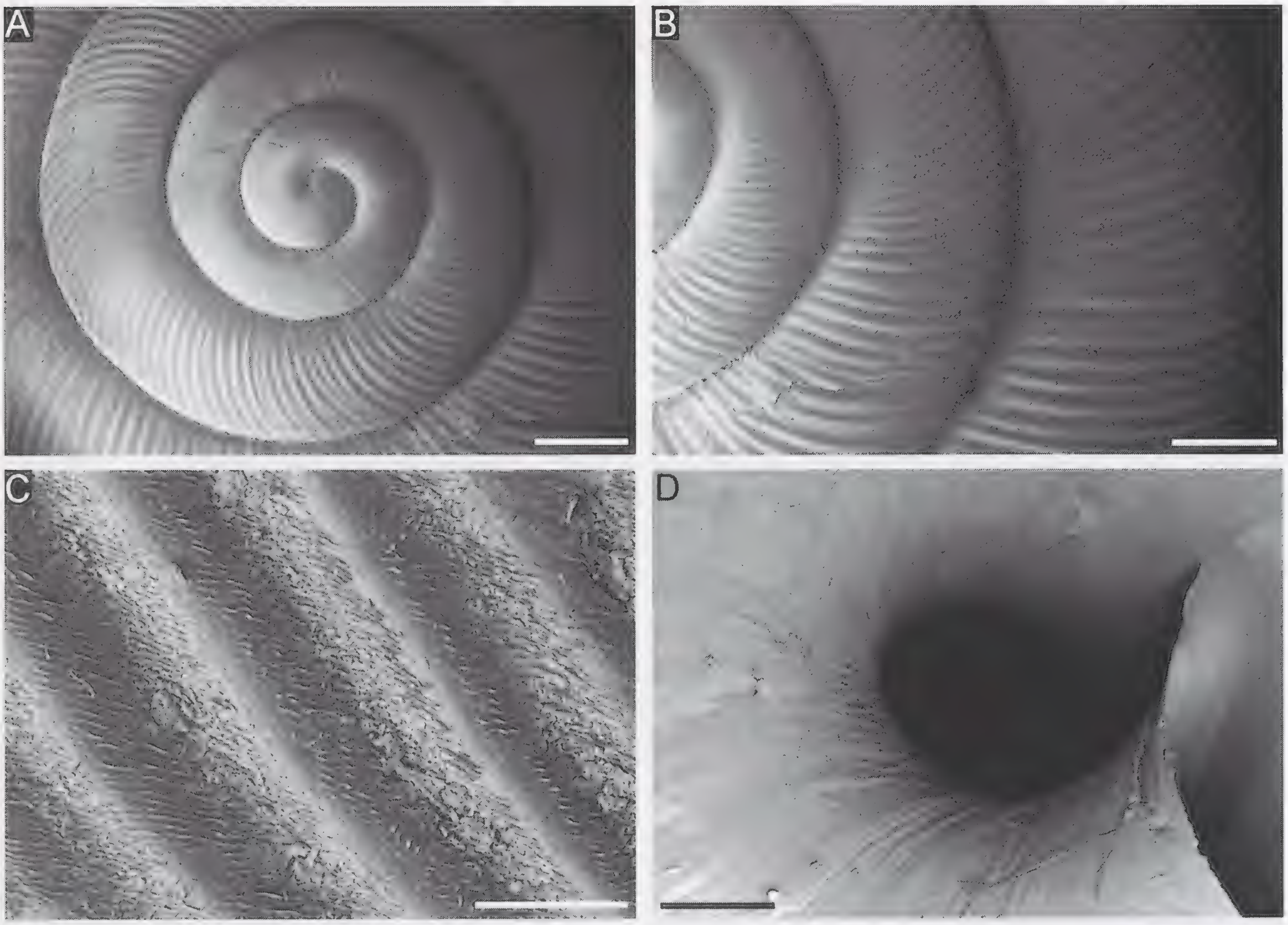

FIG. 174. SEM micrographs of the shell of ***Torresitrachia brookei*** n. sp. paratype AM C471769 (Boongaree Island). A: Apical view showing protoconch and first whorls; B: Sculpture across entire shell viewed from above. Scale bars A–B = 1 mm; C: Close-up of sculpture on last whorl. Scale bar = 200 µm; D: Umbilicus. Scale bar = 500 µm.

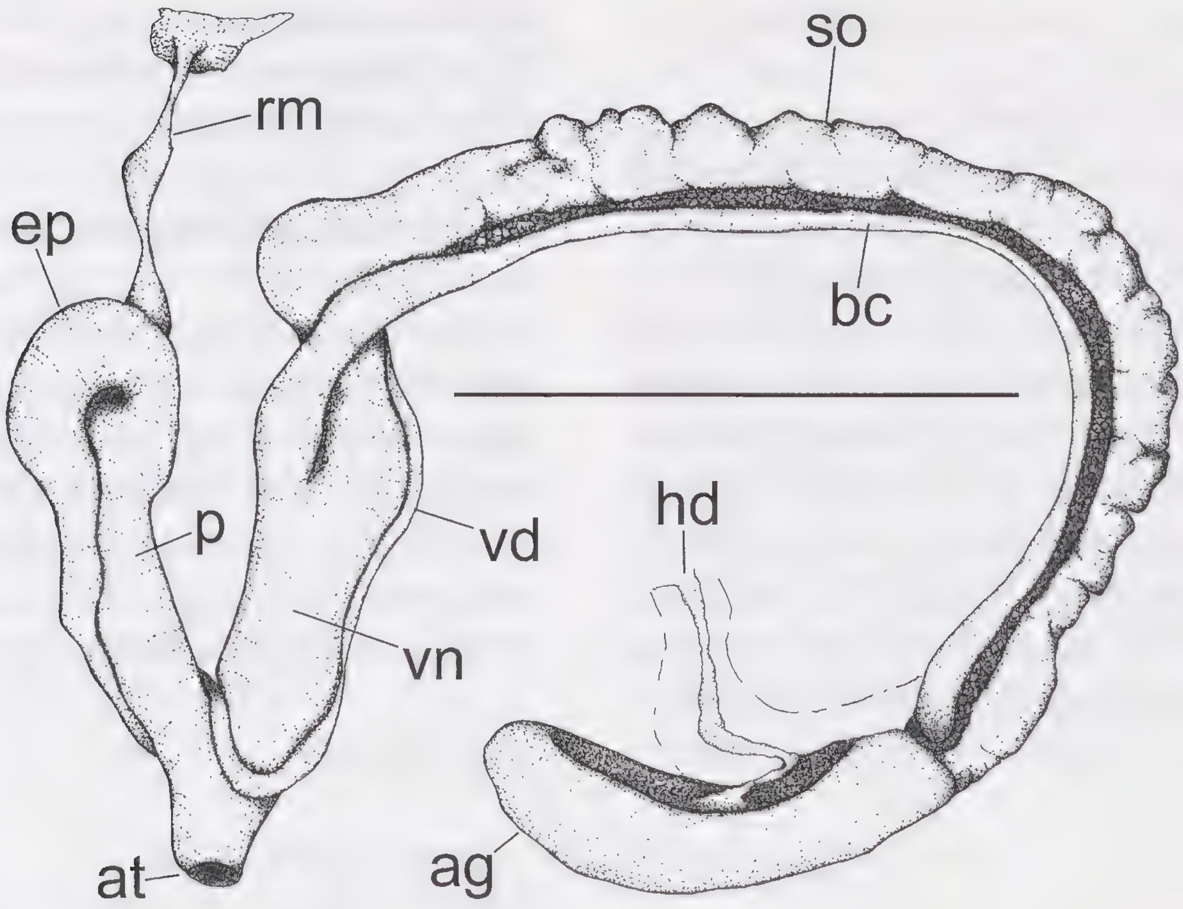

FIG. 175. Genital anatomy of ***Torresitrachia brookei*** n. sp. paratype AM C471766 (Boongaree Island, August). Scale bar = 3 mm.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.0–0.001; interspecific genetic distances: 0.095–0.142 with respect to ***T. brookei***, *T. houtmani*, ***T. eclipsis*** and ***T. janszi***; 0.206 to 0.237 to all other congeners.

Comparative Remarks

Species was listed by Solem (1991) as "*Torresitrachia* NSP2". Shell smaller than that of ***T. janszi***, differs from ***T. aquilonia*** and ***T. eclipsis*** by lack of ribs within the umbilicus; lip more weakly expanded than in ***T. aquilonia***. Penial morphology similar to *T. amaxensis* and ***T. aquilonia*** with respect to distribution of pustules and pilasters (*T. amaxensis* with larger, hooked pustules and stronger pilasters, ***T. aquilonia*** with not as regularly arranged pustules, weaker pilasters).

Distribution

Bigge Island.

Torresitrachia brookei n. sp.

Figs. 161E, 174–176

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04'14"S, 125°10'58"E; coll. Michael Shea, 8/08/2007, KIS 1–29 (dry woodland with mixed deciduous trees and shrubs; aestivating in soil between rocks).

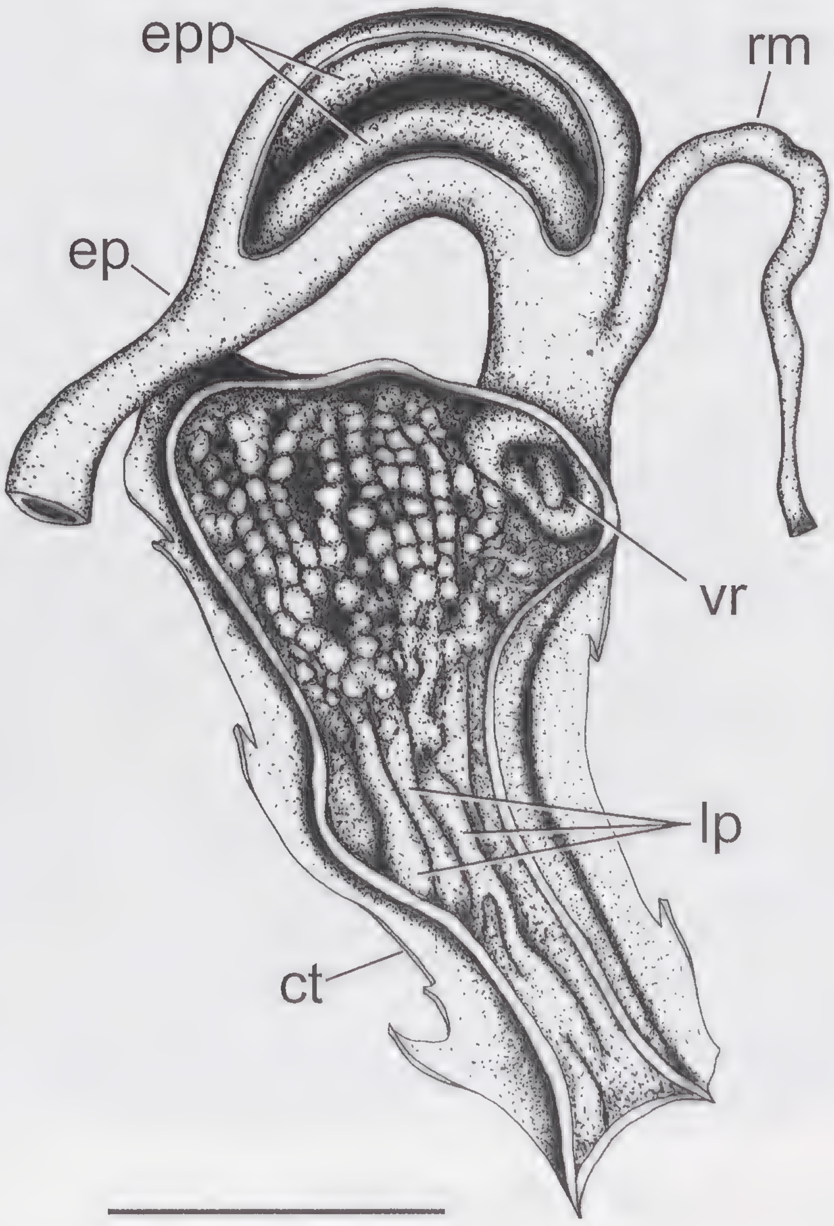

FIG. 176. Penial anatomy of ***Torresitrachia brookei*** n. sp. paratype AM C471766 (Boongaree Island, August). Scale bar = 1 mm.

Material Examined

Holotype WAM S36735 (preserved specimen, Fig. 161E). Paratypes AM C471766 (3 preserved specimens), WAM S36734 (10 preserved specimens), AM C471767 (3 shells), WAM S36432 (7 shells) from 15°04'21"S, 125°11'06"E; AM C471768 (3 shells), WAM S36433 (6 shells) from 15°04'26"S, 125°10'46"E; WAM S36434 (2 shells) from 15°04'22"S, 125°10'56"E; WAM S36435 (2 shells) from 15°04'08"S, 125°11'05"E; AM C471769 (3 shells), WAM S36436 (4 shells) from 15°04'09"S, 125°10'49"E; WAM S37647 (2 preserved specimens) 15°04'30"S, 125°11'21"E.

Etymology

In honour of John Brooke, amongst the first Englishman to arrive in Australia on board of the *Trial*, which was wrecked in May 1622 in northwestern Australia; noun in genitive case.

Description

Shell (Figs. 161E, 174): Moderate in size (D = 12.2–17.3 mm; Table 10), broadly conical with weakly to moderately elevated spire; umbilicus ~ 2 mm wide; colour brownish, not glossy. Protoconch ~ 2.0 mm in diameter, comprising about one whorl, essentially smooth. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls with sparsely covered with fine periostracal pustules. Apertural lip sharp, rather weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 175–176): Penis about as long as vagina, straight. Epiphallus about same length, with tiny epiphallic flagellum. Distal half of inner penial wall with small, roundish pustules, loosely arranged in rather irregular pattern; proximal half with indistinct longitudinal pilasters. Inner epiphallic wall with two large longitudinal pilasters. Penial retractor muscle moderately long. Vagina longer than free oviduct, inflated. Free oviduct short, S-shaped. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.001; interspecific genetic distances: 0.107–0.157 with respect to ***T. brookei***, *T. dampieri*, ***T. eclipsis*** and ***T. janszi***; 0.203 to 0.236 to all other congeners.

Comparative Remarks

Shell most similar with ***T. urvillei*** and ***T. eclipsis***. Umbilicus narrower than in ***T. eclipsis***, which also has a glossy shell. Penial anatomy similar to ***T. urvillei***, *T. amaxensis* and ***T. aquilonia*** but differing in relative size, shape and arrangement of pustules and development of longitudinal pilasters.

Distribution

Boongaree Island.

Torresitrachia bathurstensis
(E. A. Smith, 1894)

Helix (*Trachia*) *bathurstensis* E. A. Smith, 1894: 93.

Torresitrachia bathurstensis – Solem, 1979: 67–71 (partim); 1985a: 922–923 (partim); 1991: 178–179 (partim).

Type Locality

Bathurst Island, as restricted by Solem (1979).

Taxonomic Remarks

The name was originally introduced for specimens from Bathurst and Heywood islands but the type locality was subsequently restricted to Bathurst Island by Solem (1979). Solem (1979) based his anatomical description on material from the Kimbolton area (~ 16°41'12"S, 123°50'13"E), on the mainland about 80 km south of Bathurst Island, assuming that both forms were conspecific. Predominantly (or even exclusively?) based on comparison of shells, Solem (1979, 1985a, 1991) assumed that this species occupies a wide range to include mainland sites up north to Doubtful Bay as well as many islands in the Buccaneer Archipelago north to Augustus Island. However, comparative study of island forms that Solem (1991) had or would have subsumed under this taxon indicated that *T. bathurstensis* represents a complex of species of which most are narrowly endemic to single islands or even portions of larger islands. While these species exhibit relatively conserved shell characters, they differ predominantly in their genital anatomy. While several island forms are herein recognised as distinct species, I suggest restricting the taxon *T. bathurstensis* to its type locality, Bathurst Island, and possibly immediately adjacent localities. The material from the Kimbolton area used to describe the anatomy of this taxon is likely to represent yet another distinct species but not *T. bathurstensis* as delineated herein. For the uncertain delimitation of the taxon, no diagnosis is given here.

Torresitrachia allouarni n. sp.

Figs. 161F, 177–179

Type Locality

Western Australia, central Kimberley coast, Brecknock Harbour, SE corner of Augustus Island, 15°23’45”S, 124°37’47”E; coll. Vince Kessner, 12/02/2009, KIS 2–71 (vine thicket patch along creek line, on steep rocky slopes in V-shaped gully, sandstone; active on ground and boulders at night after rain).

Material Examined

Holotype. WAM S58455 (preserved specimen, Fig. 161F). Paratypes AM C471770 (4 preserved specimens), WAM S37655 (9 preserved specimens), AM C471771 (2 shells), WAM S49009 (3 shells) from type locality.

Additional, non-type material. WAM S37010 (preserved specimens) from southern section of Augustus Island, 15°23’53”S, 124°36’03”E, WAM S37011 (preserved specimens) from 15°24’02”S, 124°36’06”E.

Etymology

In honour of François-Alesno de St. Allouarn, the first French explorer to arrive in Western Australia in March 1772, near Shark Bay; noun in genitive case.

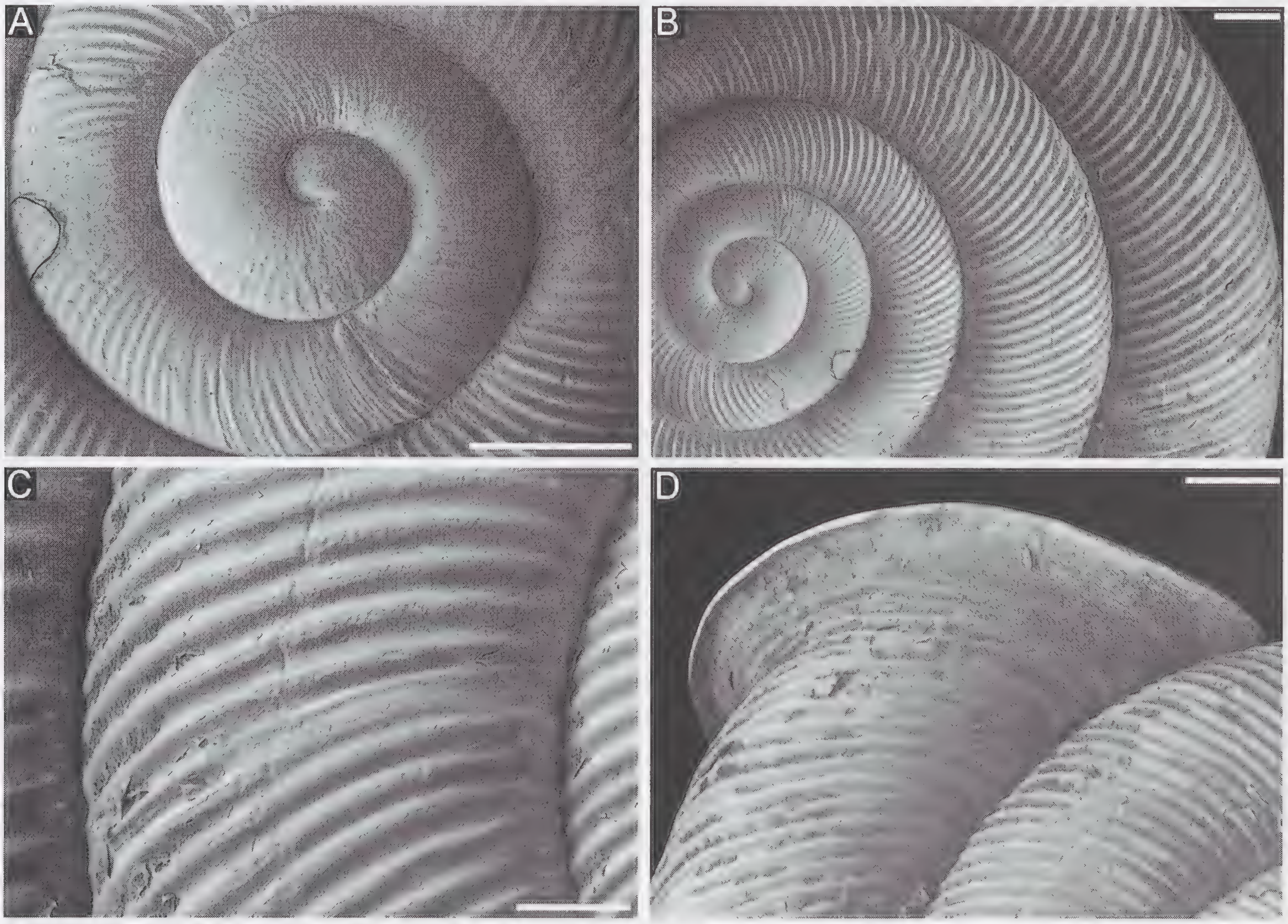

FIG. 177. SEM micrographs of the shell of ***Torresitrachia allouarni*** n. sp. paratype AM C471771 (SE Augustus Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on penultimate whorl; D: Close-up of sculpture on last whorl near aperture. Scale bars A–B, D = 1 mm; C = 500 µm.

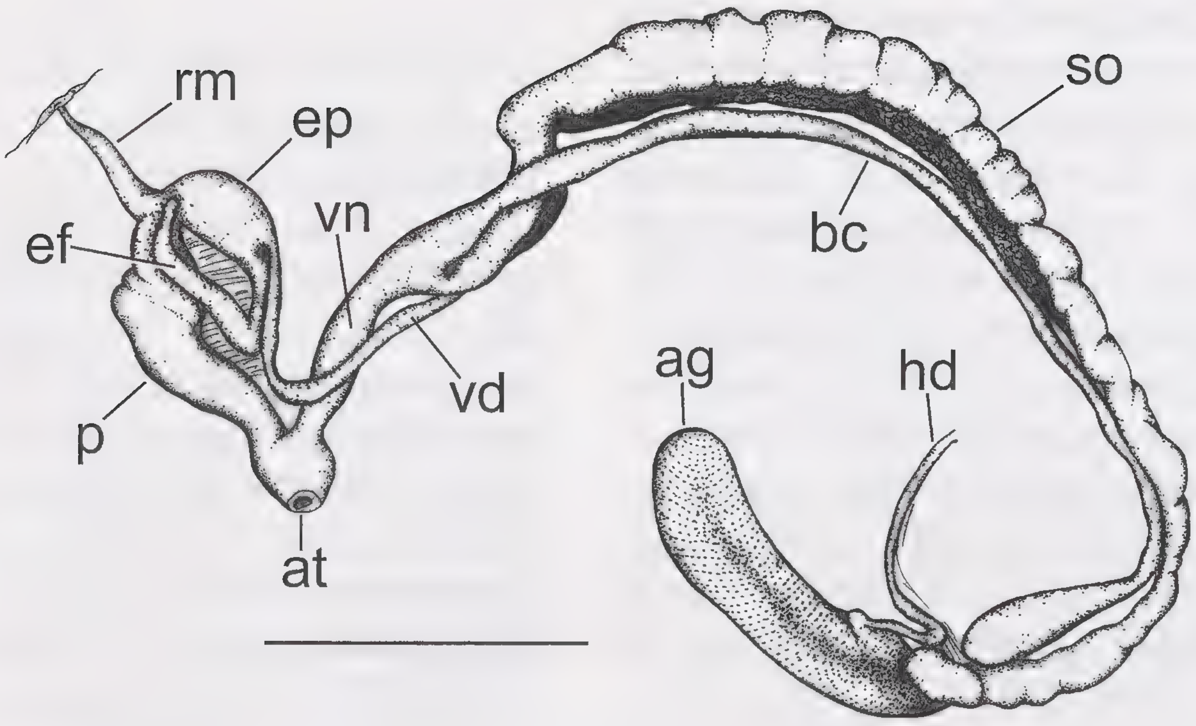

FIG. 178. Genital anatomy of ***Torresitrachia allouarni*** n. sp. paratype AM C471770 (SE Augustus Island, February). Scale bar = 5 mm.

Description

Shell (Figs. 161F, 177): Moderate in size (D = 14.7 mm on average; Table 10), discoidal to very broadly conical with almost flat to weakly elevated spire; umbilicus ~ 3 mm wide; colour brownish horn. Protoconch ~ 2.3 mm in diameter, comprising about one whorl, with weak radial pustulation. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls essentially smooth, very sparsely covered with periostracal pustules; fine pustules directly underneath suture. Apertural lip sharp to thickened, weakly to well expanded, weakly reflected, well rounded without nodes, parietal wall extremely delicate.

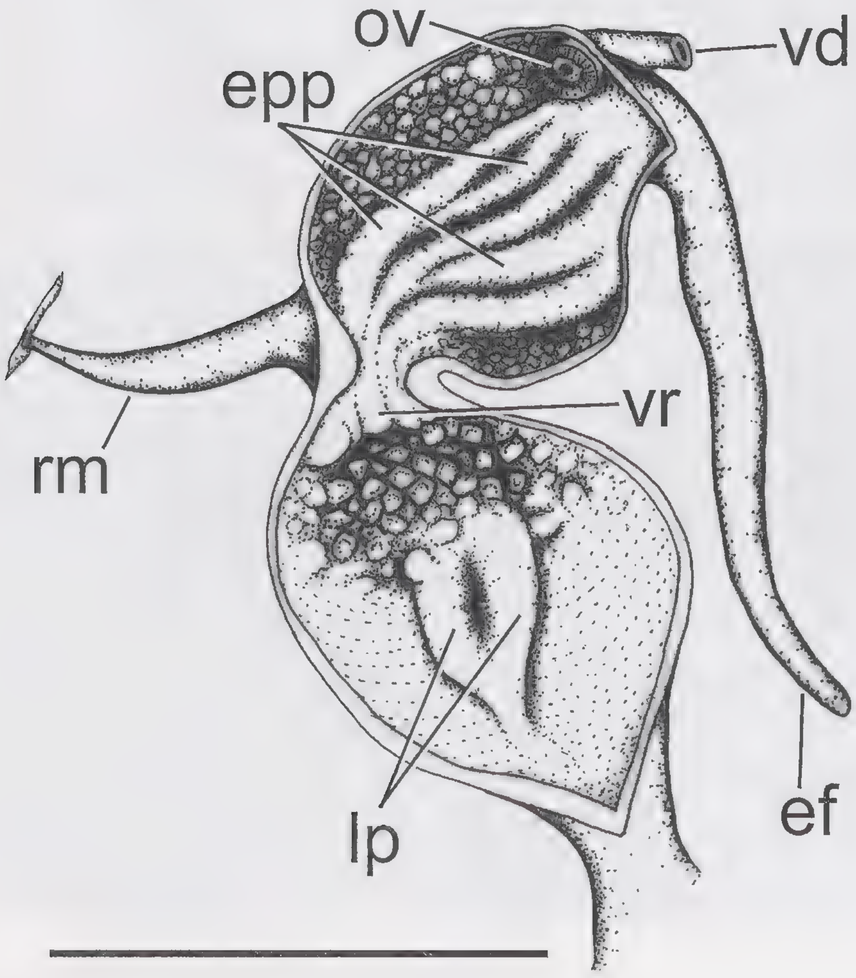

FIG. 179. Penial anatomy of ***Torresitrachia allouarni*** n. sp. paratype AM C471770 (SE Augustus Island, February). Scale bar = 3 mm.

Genital anatomy (Figs. 178–179): Penis as long as vagina, straight. Epiphallus about same length, with long, narrow epiphallic flagellum. Distal end of inner penial wall with few, small, pustules, densely arranged in honeycomb pattern; most of inner wall smooth with two well-defined longitudinal pilasters, situated next to each other and fused at either end. Inner epiphallic wall with five longitudinal pilasters, rest of epiphallic wall covered with dense, fine pustulation. Penial retractor muscle short. Vagina about same length as free oviduct, tubular. Free oviduct moderately long. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (4 sequences): 0.004–0.010; interspecific genetic distances: 0.049–0.052 with respect ***T. tasmani***; 0.091–0.094 to ***T. baudini***, 0.094–0.101 to ***T. flindersi***; 0.114–0.135 to ***T. aquilonia***, ***T. freycineti***, ***T. girgarinae***, ***T. hartogi*** and ***T. leichhardti***; 0.217–0.230 to all other congeners.

Comparative Remarks

Shell flatter than in all species treated above, which figures in a lower H/D ratio (Table 10);

protoconch with pustulation instead of smooth. Genetically most similar species are found in adjacent areas, such as ***T. tasmani*** (Byam Martin Island), ***T. flindersi*** (NW part of Augustus Island), ***T. baudini*** (islet SE of Augustus Island), all of which are assumed to form a flock of closely related species. ***Torresitrachia allouarni*** reveals distinctive genital features that are not known from any other species, such as pustulation of epiphallic wall and closely adjacent pair of partly fused longitudinal pilasters on inner penial wall. These distinctive features are considered to be indicative of status as distinct species.

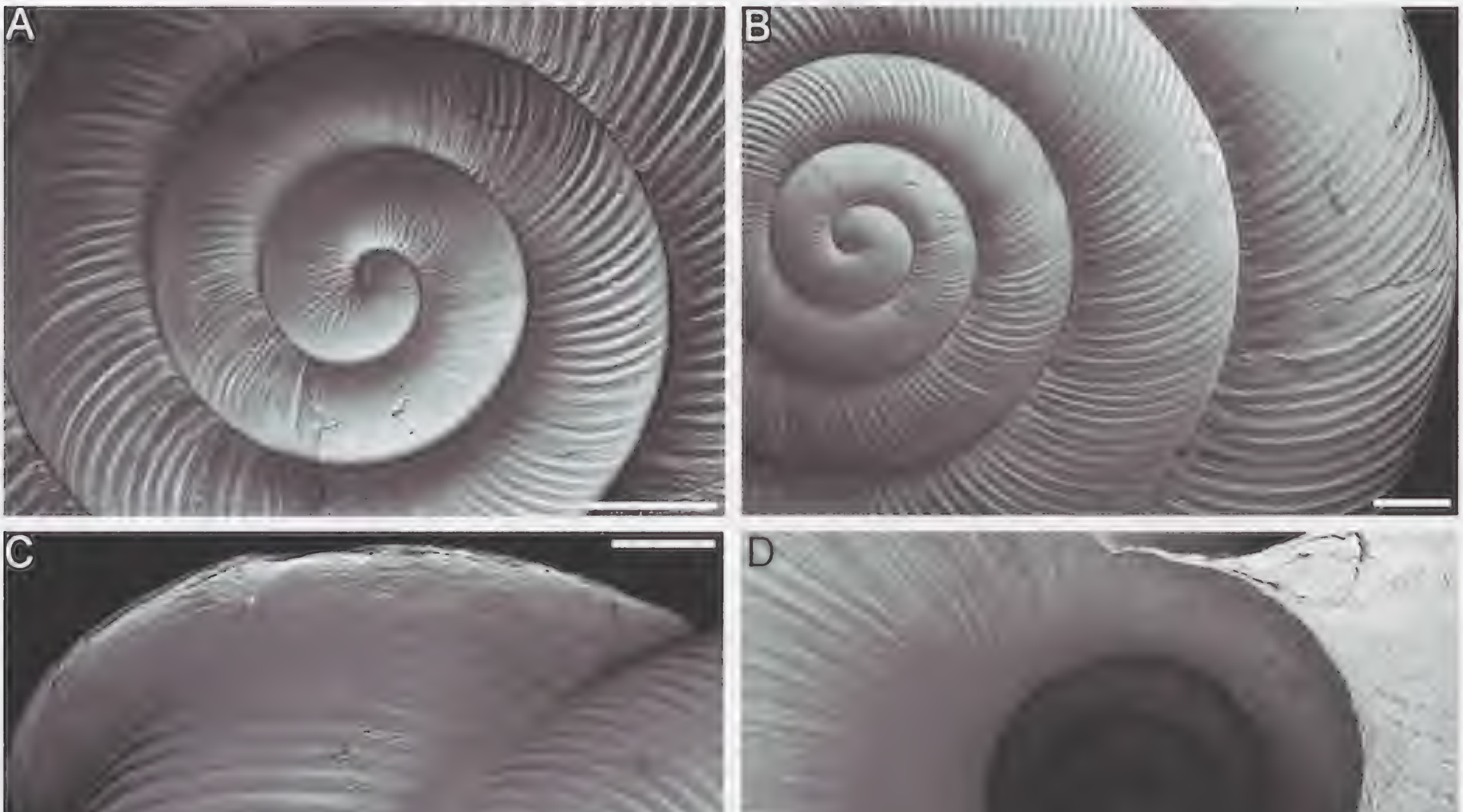

FIG. 180. SEM micrographs of ***Torresitrachia flindersi*** n. sp. (NW Augustus Island). A–D: Shell paratype AM C471775. Scale bars = 1 mm. A: Apical view showing protoconch and first whorls; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl near aperture; D: Umbilicus; E–F: Radula paratype AM C471772. Scale bars = 50 µm; E: Central and lateral teeth viewed from above; F: Marginal teeth viewed obliquely from above.

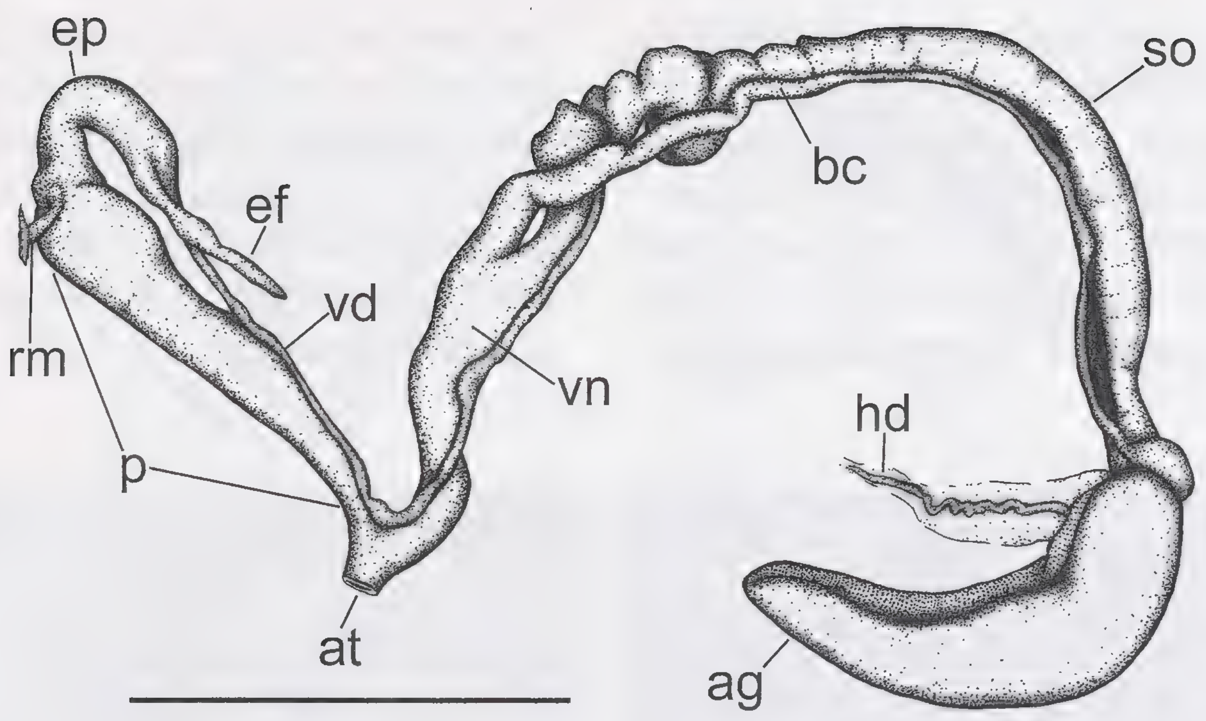

FIG. 181. Genital anatomy of ***Torresitrachia flindersi*** n. sp. paratype AM C471772 (NW Augustus Island, May). Scale bar = 5 mm.

Distribution

Southeastern portion of Augustus Island. Not found in northern Augustus Island, which is occupied by ***T. flindersi***.

Torresitrachia flindersi n. sp.
Figs. 161G–H, 180–182

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, NW section of Augustus Island, 15°19'58"S, 124°31'01"E; coll. Michael Shea, 26/05/2008, KIS 1–51 (vine thicket on S-facing rocky slope below sandstone escarpment; inside logs and *Pandanus* stumps on lower slopes).

Material Examined

Holotype WAM S58456 (preserved specimen, Fig. 161G). Paratypes AM C471772 (7 preserved specimens), WAM S37022 (12 preserved specimens), AM C471773 (7 shells), WAM S37282 (14 shells) from type locality; AM C471774 (6 preserved specimens), WAM S37648 (18 preserved specimens) from 15°20'11"S, 124°31'10"E; AM C471775 (5 shells), WAM S37281 (9 shells) from 15°20'04"S, 124°31'01"E; WAM S37021 (5 preserved specimens) from 15°20'04"S, 124°31'01"E.

Additional, non-type material. WAM S37278 (9 shells) from 15°21'05"S, 124°31'36"E; AM C471776 (4 shells), WAM S37277 (12 shells) from 15°21'05"S, 124°31'47"E; WAM S37276 (10 shells) from 15°20'59"S, 124°31'30"E; WAM S37275 (5 shells) from 15°21'06"S, 124°31'48"E; WAM S37279 (9 shells) from 15°21'24"S, 124°31'39"E; WAM S37220 (5 preserved specimens), WAM S37280 (9 shells) from 15°20'16"S, 124°31'16"E.

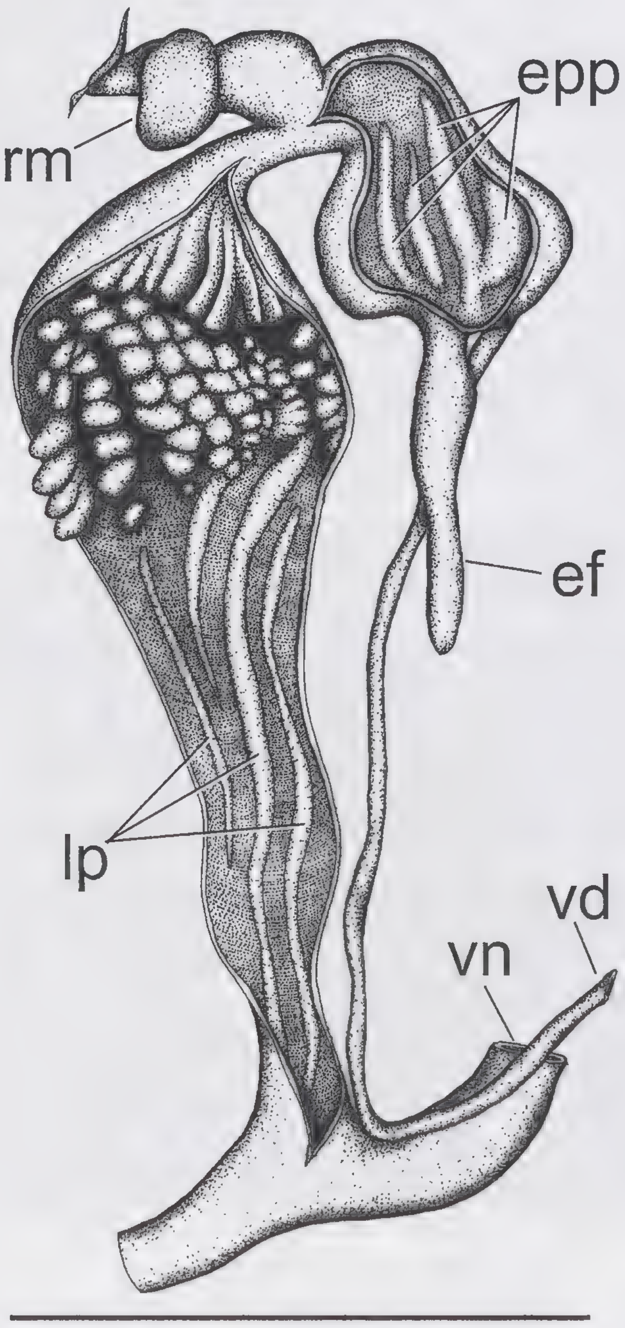

FIG. 182. Penial anatomy of ***Torresitrachia flindersi*** n. sp. paratype AM C471772 (NW Augustus Island, May). Scale bar = 3 mm.

Etymology

In honour of Matthew Flinders, who circumnavigated Australia together with George Bass in 1798–99; noun in genitive case.

Description

Shell (Figs. 161G, H, 180A–D): Moderate in size (D = 6.6 mm on average; Table 10), discoidal to very broadly conical with almost flat to weakly elevated spire; umbilicus ~ 3 mm wide; colour brownish horn. Protoconch ~ 2.4 mm in diameter, comprising about one whorl, with weak, radially arranged pustulation. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls essentially smooth, very sparsely covered with periostracal pustules. Apertural lip sharp, rather weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Radula (Fig. 180E, F): C + 12–13 + 3–4 + 16–18 (n = 1).

Genital anatomy (Figs. 181–182): Penis longer than vagina, straight. Epiphallus tiny, much shorter than penis, with long, narrow epiphallic flagellum. Distal third of inner penial wall with very large, roundish pustules, loosely arranged in longitudinal rows; proximal two thirds with four to five well-defined longitudinal pilasters, only two of them reaching proximal end. Inner epiphallic wall with four to five well-defined longitudinal pilasters, only two of them reaching proximal end. Penial retractor muscle moderate. Vagina about same length as free oviduct. Free oviduct moderately long, coiled. Bursa copulatrix with conspicuously inflated head, reaching anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.015; interspecific genetic distances: 0.037–0.038 with respect to ***T. baudini***; 0.079–0.080

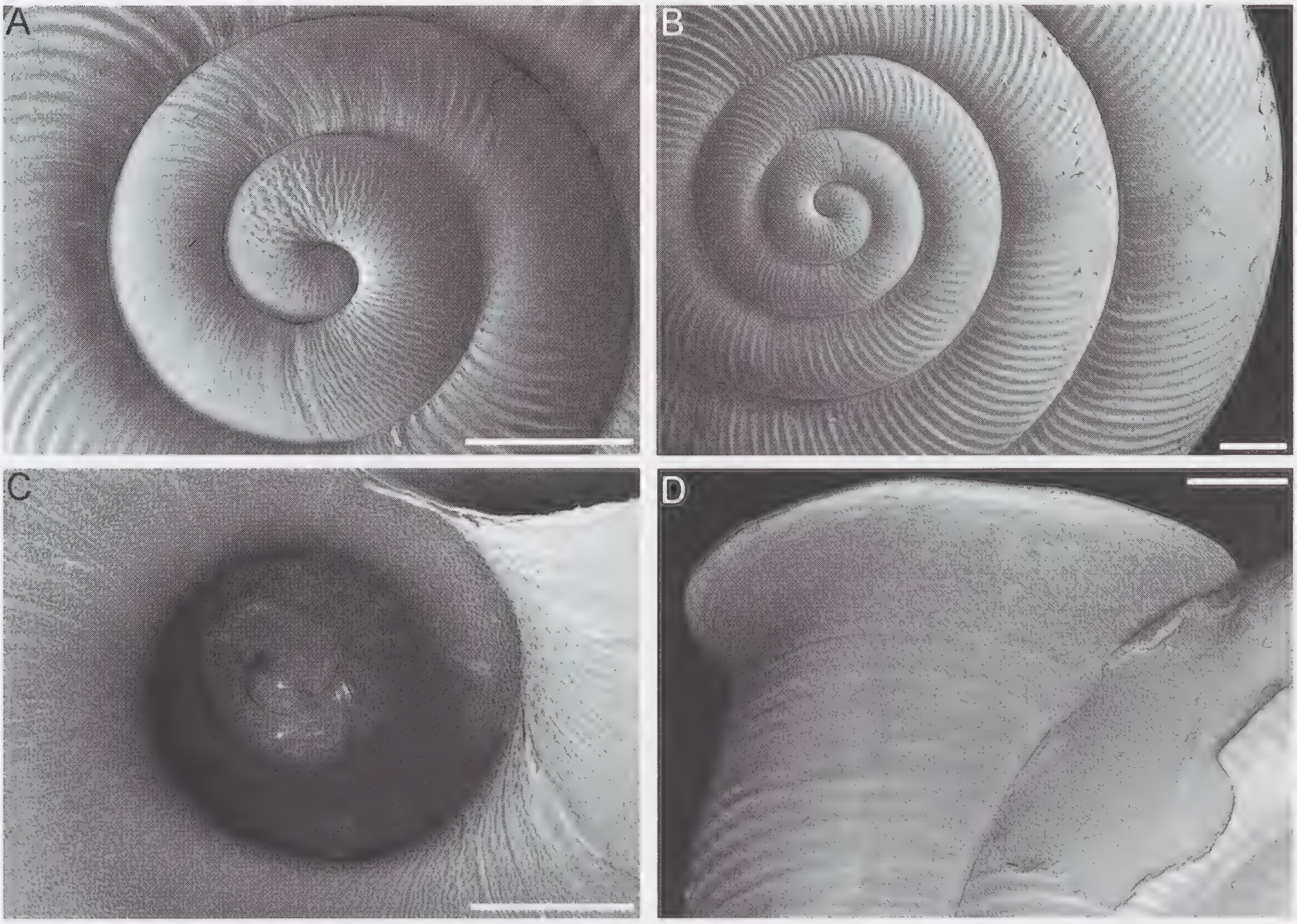

FIG. 183. SEM micrographs of the shell of ***Torresitrachia baudini*** n. sp. paratype AM C471778 (islet SE of Augustus Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Umbilicus; D: Close-up of sculpture on last whorl near aperture. Scale bars = 1 mm.

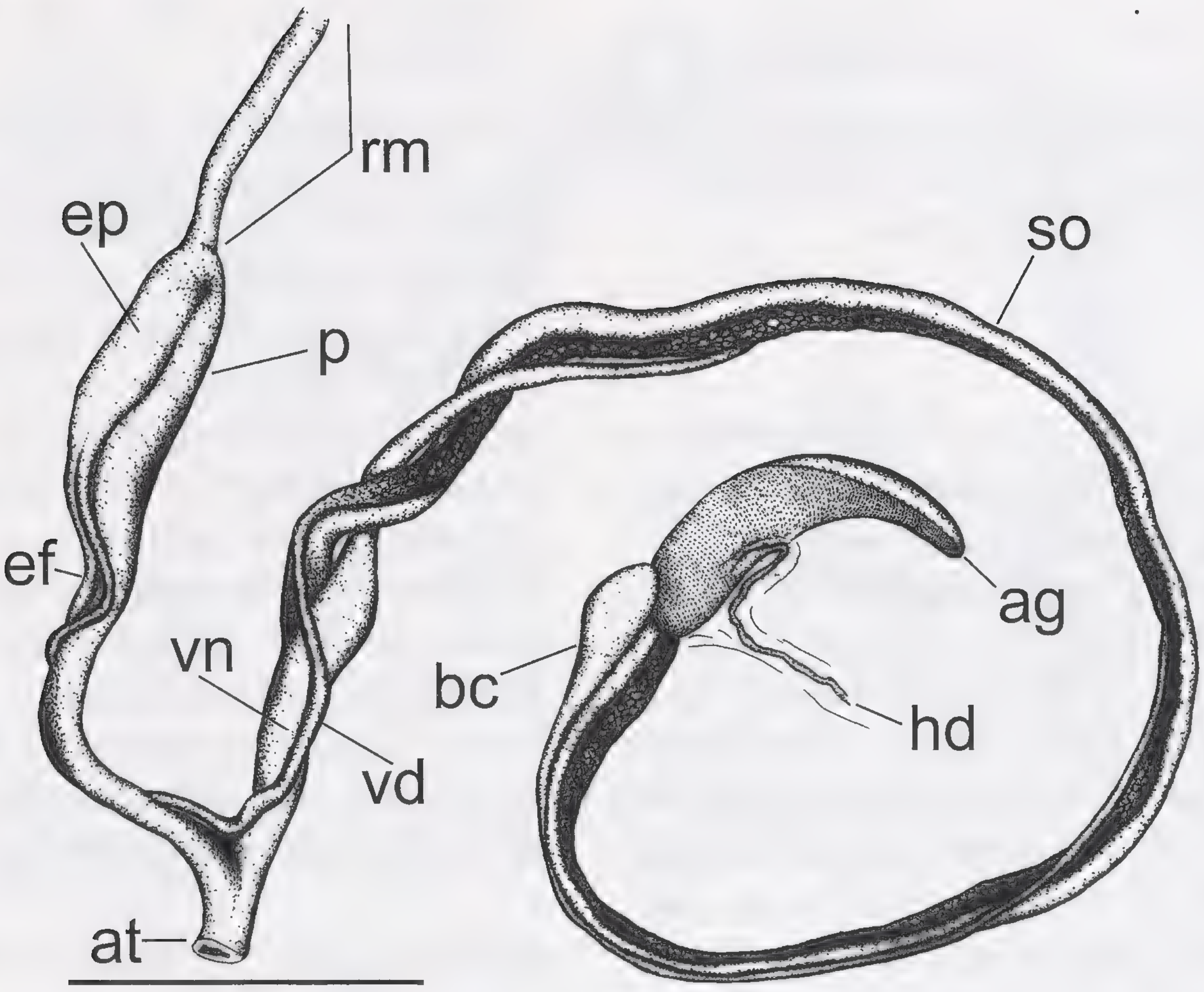

FIG. 184. Genital anatomy of **Torresitrachia baudini** n. sp. paratype AM C471777 (islet SE of Augustus Island, February). Scale bar = 3 mm.

to ***T. tasmani***, 0.094–0.101 to ***T. allouarni***; 0.109–0.135 to ***T. aquilonia***, ***T. freycineti***, ***T. girgarinae***, ***T. hartogi*** and ***T. leichhardti***; 0.217–0.230 to all other congeners.

Comparative Remarks

Most similar to ***T. allouarni***, both species having comparatively flat shells (i.e., low H/D ratio, Table 10); protoconch with pustulation instead of smooth. Both species belong to a complex of species that are separated by relatively low genetic distances of about 0.05 to 0.10. Genetically most similar is ***T. baudini***. It differs by more extended pustulation and not as well-developed longitudinal pilasters of inner penial wall; for comparison with ***T. allouarni*** see above. In general, penial wall sculpture is similar to ***T. aquilonia*** (with smaller pustules, indistinct pilasters), ***T. urvillei*** (smaller pustules, broader and fewer pilasters), and ***T. brookei*** (smaller pustules and indistinct pilasters). Typical of ***T. flindersi*** are rhomboid, elongate shape of pustules, pustulation being restricted to distal quarter of inner penial wall, straight and narrow pilasters along most of penial and epiphallic wall.

Distribution

Northwestern section of Augustus Island, not found in southern portion of the island, which is occupied by ***T. allouarni***.

Torresitrachia baudini n. sp.

Figs. 161I, 183–185

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Brecknock Harbour, small unnamed island SE of Augustus Island, 15°22'22"S, 124°37'50"E; coll. Vince Kessner, 12/02/2009, KIS 2–70 (vine thicket patch on steep slope above beach, sandstone; under rocks and logs).

Material Examined

Holotype WAM S58457 (preserved specimen, Fig. 161I). Paratypes AM C471777 (3 preserved specimens), WAM S37653 (9 preserved specimens), AM C471778 (15 shells), WAM S49003 (28 shells).

Etymology

In honour of Nicolas Baudin, who lead until then the largest scientific expedition to Western Australia in 1800–1801 on board the ships *Le Géographe* and *Le Naturaliste*; noun in genitive case.

Description

Shell (Figs. 161I, 183): Rather large (D = 14.8–17.5 mm; Table 10), broadly conical with

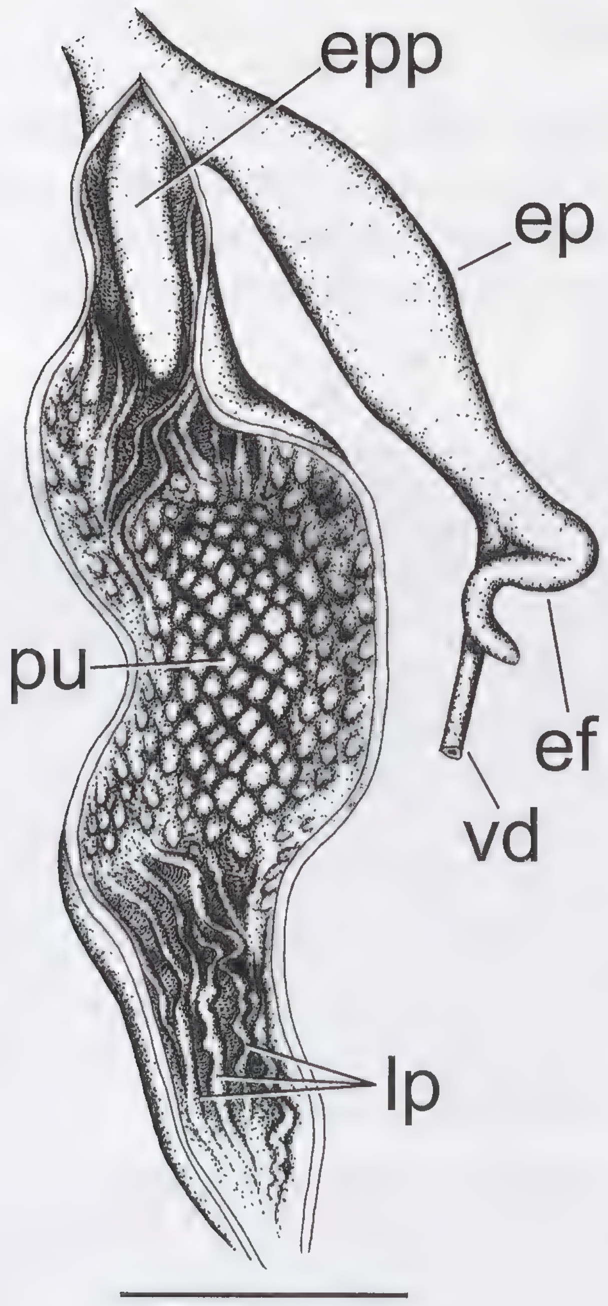

FIG. 185. Penial anatomy of ***Torresitrachia baudini*** n. sp. paratype AM C471777 (islet SE of Augustus Island, February). Scale bar = 1 mm.

weakly to moderately elevated spire; periphery well rounded to slightly angled, suture shallow; umbilicus ~ 3 mm wide; colour light yellowish-brown to horn. Protoconch ~ 2.3 mm in diameter, comprising about one whorl, with weakly developed radial pustulation. Teleoconch with fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls essentially smooth, very sparsely covered with periostracal pustules; fine pustules directly underneath suture. Apertural lip sharp, weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 184–185): Penis longer than vagina, tubular, straight. Epiphallus about half as long as penis, with very long, narrow epiphallic flagellum. Distal half of inner penial wall with large, rhomboid pustules, densely arranged in honeycomb pattern; proximal third with five or more thin, partly undulating longitudinal pilasters. Inner epiphallic wall with five or more thin, partly undulating longitudinal pilasters. Penial retractor muscle long. Vagina longer than free oviduct, tubular. Free oviduct moderately long, coiled. Bursa copulatrix with inflated head, extending anterior end of albumen gland.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.077 with respect to ***T. flindersi***; 0.079–0.080 to ***T. tasmani***, 0.091–0.094 to ***T. allouarni***; 0.109–0.135 to ***T. aquilonia, T. freycineti***, ***T. girgarinae***, ***T. hartogi*** and ***T. leichhardti***; 0.217–0.230 to all other congeners.

Comparative Remarks

Similar to ***T. allouarni*** and ***T. flindersi***, shell is rather flat but more elevated and larger than in the former two species. Protoconch of ***T. baudini*** is comparatively small and has a stronger pustulation than in previous species. Genetic distance to ***T. flindersi*** is low and not necessarily indicative of distinct species status. However, penial anatomy reveals distinct features that are considered sufficient to treat both as separate species (area of pustulation of penial wall extends much further in ***T. baudini*** than in ***T. flindersi***, distal and proximal portions of wall with many delicate and undulating pilasters). Because these differences are of qualitative but not quantitative nature, they are unlikely to be attributed to seasonal or individual variation in development of structures.

Distribution

Islet southeast of Augustus Island.

Torresitrachia tasmani n. sp.

Figs. 161J, 186–188

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, Byam Martin Island, 15°23’09”S, 124°21’42”E; coll. Michael Shea, 3/06/2008, KIS 1–61 (dry vine thicket patches, eucalypts on S-facing slope, sandstone; under rocks).

Material Examined

Holotype WAM S58458 (preserved specimen, Fig. 161J). Paratypes AM C471779 (15 preserved specimens), WAM S37026 (36 preserved specimens), WAM S37649 (5 preserved specimens), AM C471780 (7 shells), WAM S37289 (17 shells), WAM S49012 (5 shells) from type locality.

Etymology

In honour of Abel Tasman, the first European explorer, who charted the Western Australian coast between Shark Bay and Cape York in 1644; noun in genitive case.

Description

Shell (Figs. 161J, 186A–D): Rather large (D = 15.9–19 mm; Table 10), broadly conical with weakly to moderately elevated spire; periphery well rounded to slightly angled, suture shallow;

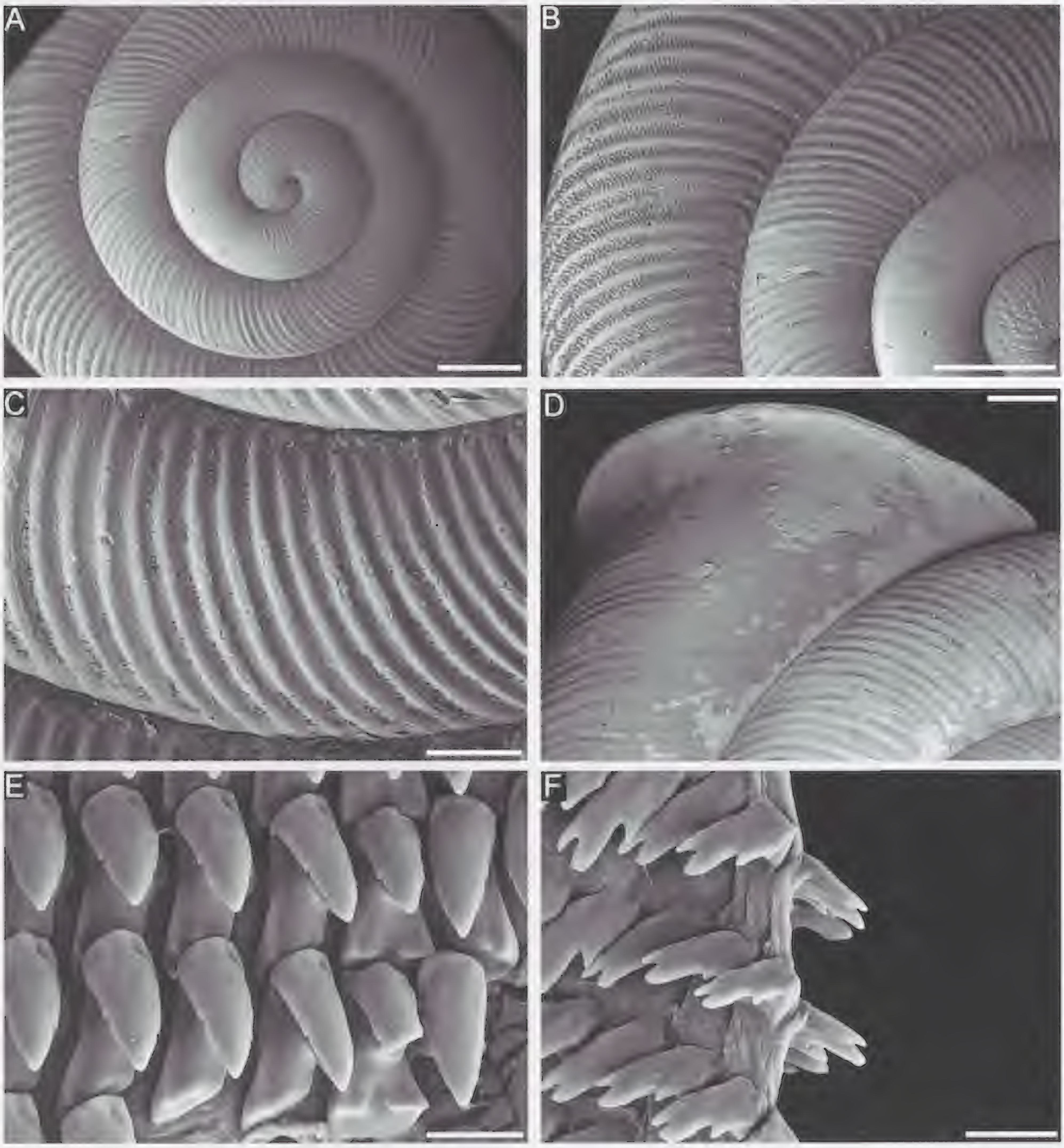

FIG. 186. SEM micrographs of ***Torresitrachia tasmani*** n. sp. (Byam Martin Island). A–D: Shell paratype AM C471780. A: Apical view showing protoconch and first whorls; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on penultimate whorl; D: Close-up of sculpture on last whorl near aperture. Scale bars A–B, D = 1 mm, C = 500 µm; E–F: Radula paratype AM C471779. Scale bars = 20 µm. E: Central and inner lateral teeth; F: Marginal teeth.

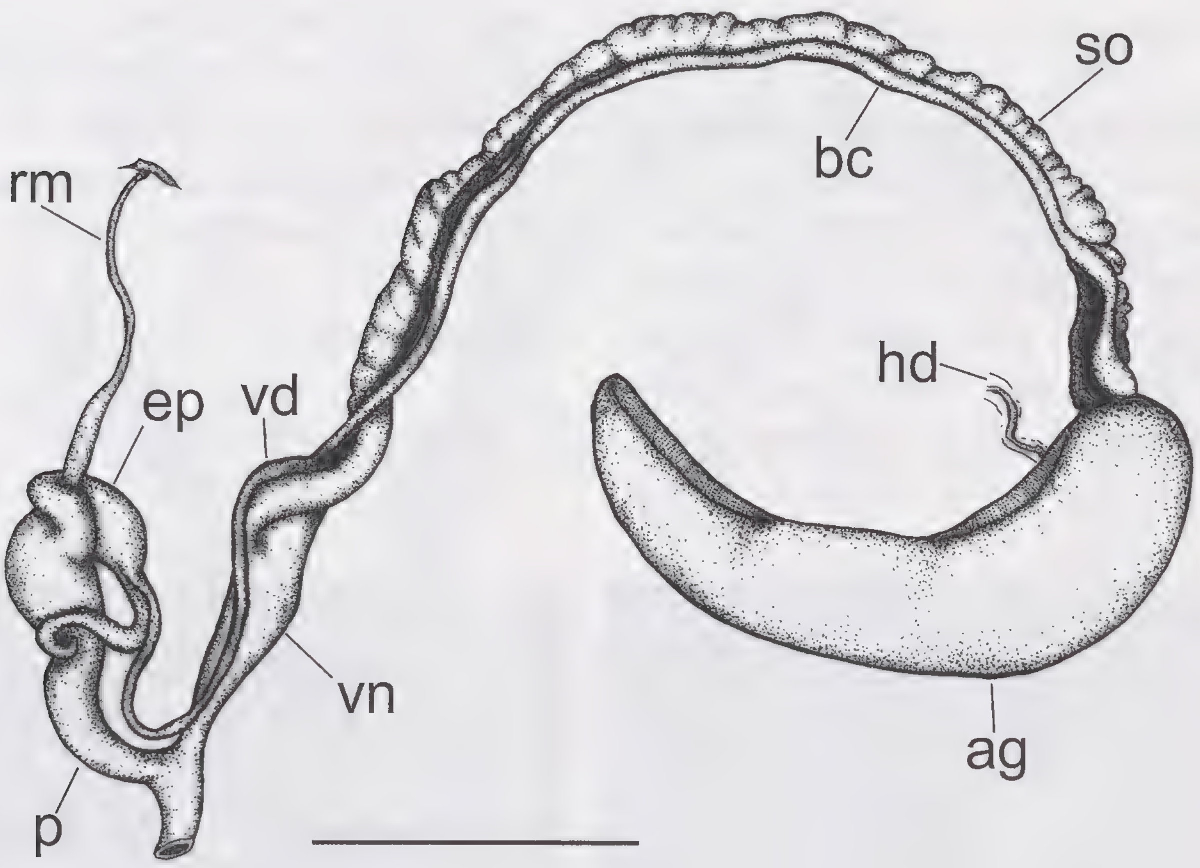

FIG. 187. Genital anatomy of ***Torresitrachia tasmani*** n. sp. paratype AM C471779 (Byam Martin Island, June). Scale bar = 3 mm.

umbilicus ~ 3 mm wide; colour yellowish-brown. Protoconch ~ 2.3 mm in diameter, comprising about one whorl, with weakly developed radial pustulation. Teleoconch with fine, regularly and narrowly spaced radial ribs, becoming indistinct below periphery and extending as weak growth lines onto base of shell; inner umbilical whorls essentially smooth, very sparsely covered with periostracal pustules; pustules directly underneath suture. Apertural lip sharp, weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Radula (Fig. 186E, F): C + 18–20 + 2–3 + 18–20.

Genital anatomy (Figs. 187–188): Penis rather as long as vagina), tubular, coiled or winding. Epiphallus slightly shorter than penis, with very long, coiled, narrow epiphallic flagellum. Distal half of inner penial wall with moderate to large, rhomboid pustules, densely arranged in honeycomb pattern; proximal half with six to seven well-developed longitudinal pilasters, two of them reaching the basal end. Inner epiphallic wall with four to five well-developed longitudinal pilasters. Penial retractor muscle long. Vagina longer than free oviduct, tubular, inner wall with longitudinal pilasters. Free oviduct short, coiled. Bursa copulatrix with inflated head, extending anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.0; interspecific genetic distances: 0.049–0.052 with respect ***T. allouarni***; 0.077 to ***T. baudini***, 0.079–0.080 to ***T. flindersi***; 0.107–0.135 to ***T. aquilonia***, ***T. freycineti***, ***T. girgarinae***, ***T. hartogi*** and ***T. leichhardti***; 0.217–0.228 to all other congeners.

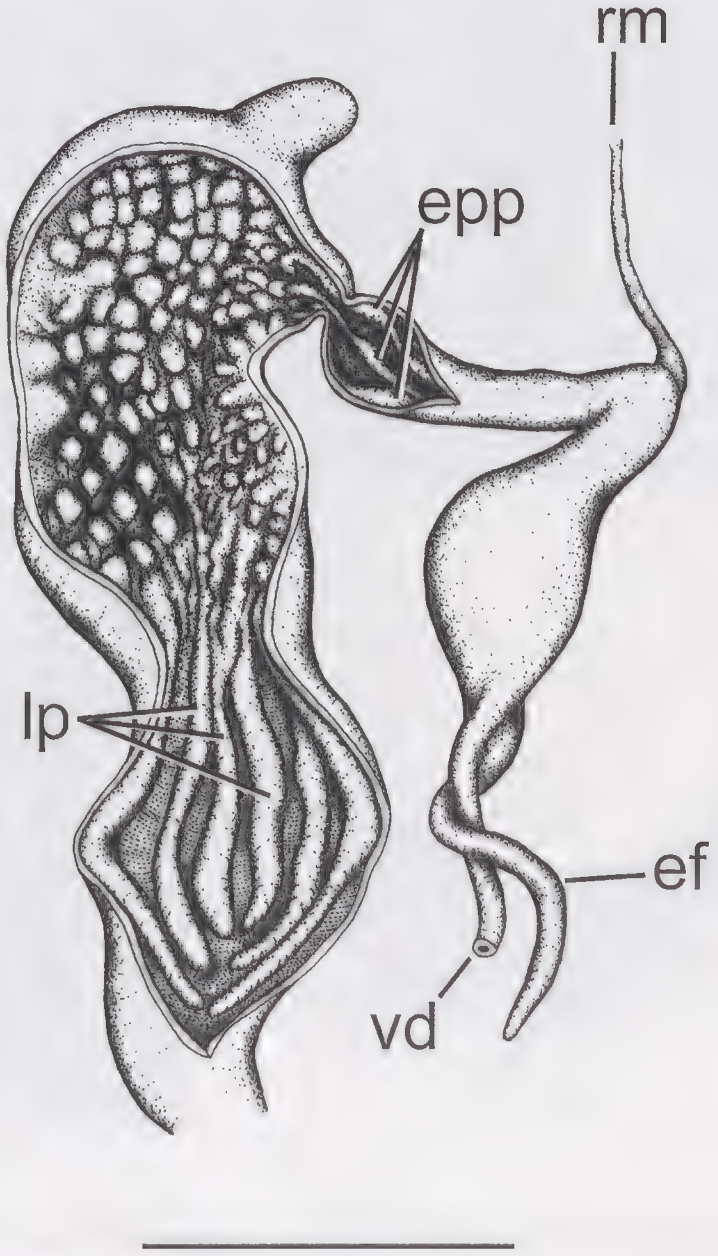

FIG. 188. Penial anatomy of ***Torresitrachia tasmani*** n. sp. paratype AM C471779 (Byam Martin Island, June). Scale bar = 1 mm.

Comparative Remarks

Shell most similar to ***T. baudini*** but differing by darker colour plus weaker pustulation of protoconch; shell larger than in most species, with wider umbilicus (except ***T. janszi*** being of similar size), with more elevated spire than ***T. allouarni*** and ***T. flindersi***. Penial anatomy most similar to ***T. flindersi*** but pustules smaller and rounded instead of rhomboid, pilasters of penial and epiphallic walls more strongly developed and closer. ***T. baudini*** differs by more extended area of pustulation and more indistinct pilasters.

Distribution

Byam Martin Island.

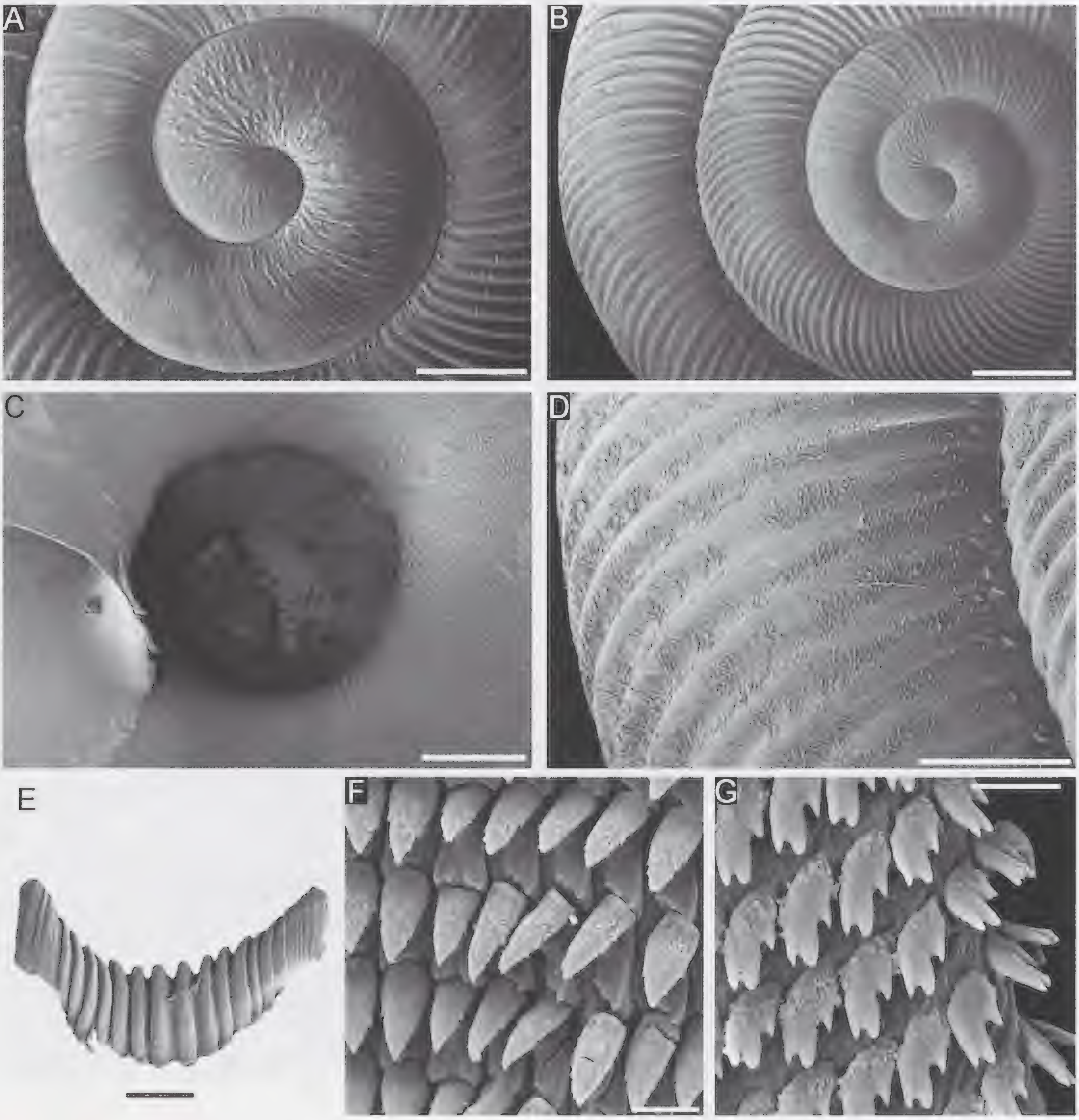

FIG. 189. SEM micrographs of ***Torresitrachia freycineti*** n. sp. (D'Arcy Island). A–D: Shell paratype AM C471783. A: Apical view showing protoconch and first whorls; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on penultimate whorl; D: Close-up of sculpture on last whorl near aperture. Scale bars A–B, D = 1 mm, C = 500 µm; E–F: Radula paratype AM C471781. Scale bars = 20 µm. E: Central and inner lateral teeth; F: Marginal teeth.

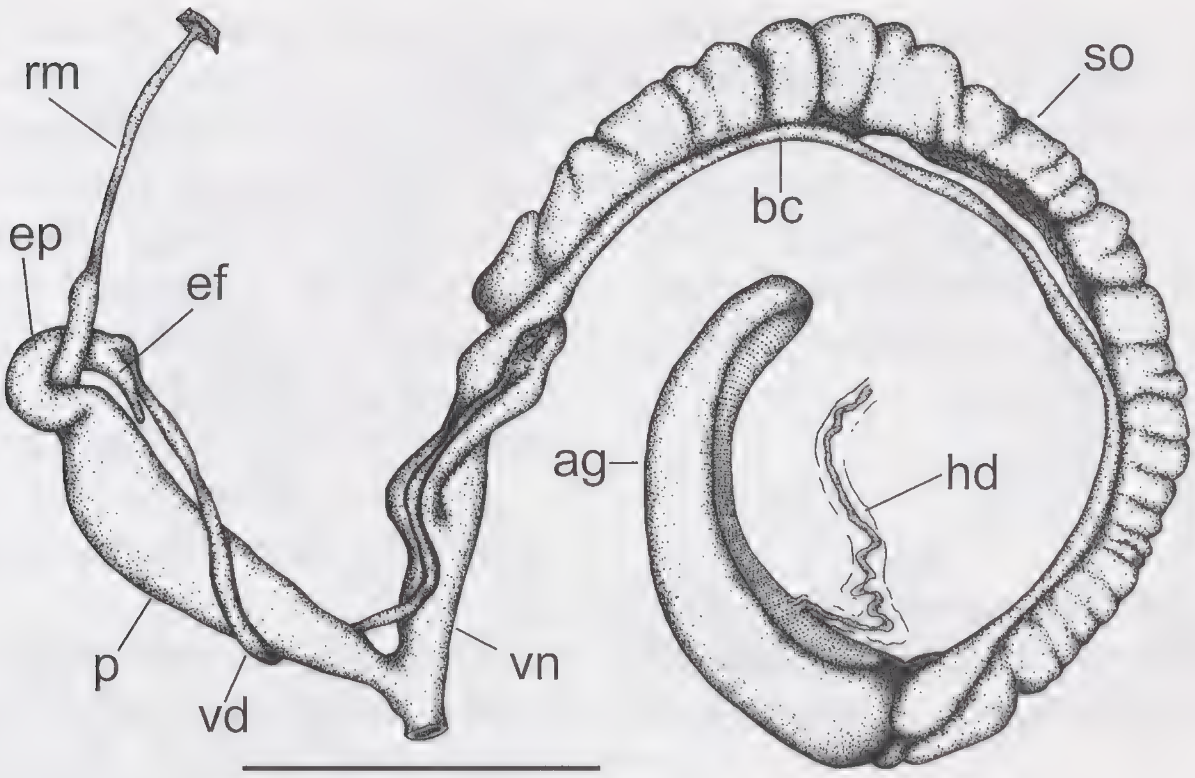

FIG. 190. Genital anatomy of ***Torresitrachia freycineti*** n. sp. paratype AM C471781 (D'Arcy Island, June). Scale bar = 5 mm.

Torresitrachia freycineti n. sp.
Figs. 161K–L, 189–191

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, NW section of D'Arcy Island, 15°15'30"S, 124°26'25"E; coll. Roy Teale, 5/06/2008, KIS 2–57 (very small vine thicket in scrubby woodland; aestivating under rocks in loose soil).

Material Examined

Holotype WAM S58459 (preserved specimen). Paratypes AM C471781 (6 preserved specimens), WAM S37015 (13 preserved specimens), WAM S37295 (11 shells) from type locality; AM C471786 (6 preserved specimens), WAM S37012 (19 preserved specimens), WAM 37292 (9 shells) from 15°15'09"S, 124°26'33"E; WAM S37296 (9 shells) from 15°15'30"S, 124°25'57"E; AM C471787 (5 preserved specimens), WAM S37018 (14 preserved specimens) from 15°15'45"S, 124°26'36"E; AM C471782 (10 preserved specimens), WAM S37651 (24 preserved specimens) AM C471783 (10 shells), WAM S49006 (15 shells) from NE section, 15°15'35"S, 124°26'36"E.

Additional, non-type material. WAM S37650 (29 preserved specimens), AM C471784 (15 preserved specimens), WAM S37013 (39 preserved specimens), WAM S37293 (24 shells), WAM S37014 (5 preserved specimens), WAM S37294 (8 shells), WAM S37016 (13 preserved specimens), WAM S37017 (5 preserved specimens), WAM S37301 (8 shells), from NW section of D'Arcy Island; WAM S37646 (preserved specimen), WAM S37283 (10 shells), AM C471787 (5 preserved specimens),

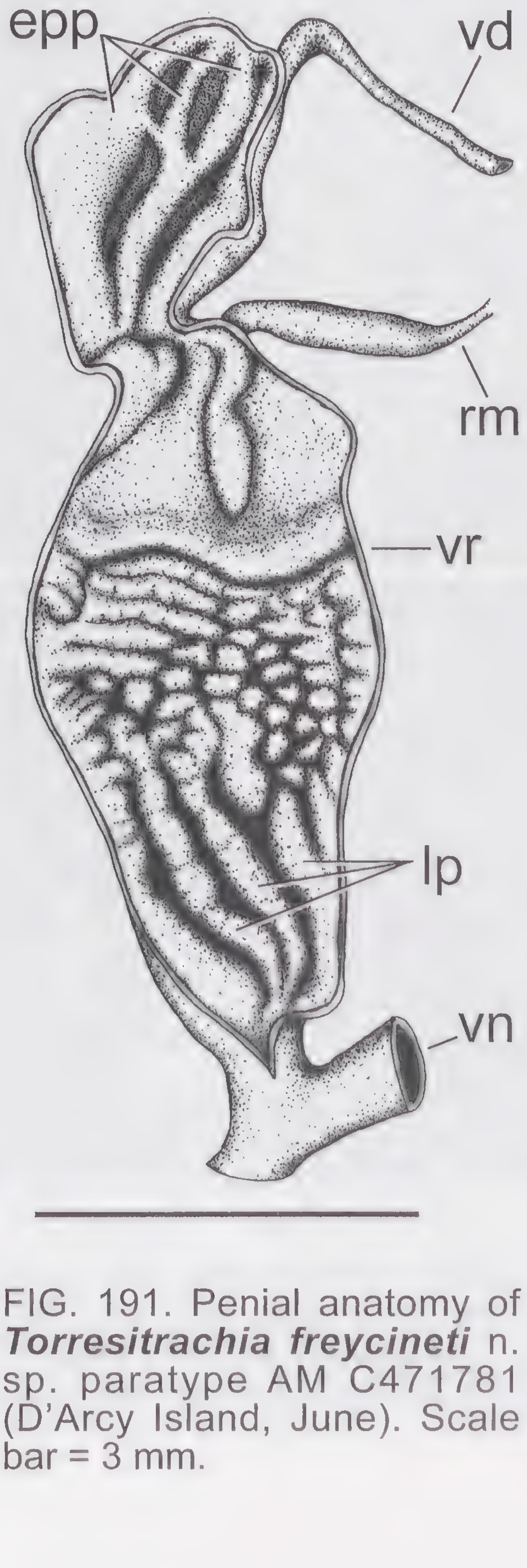

FIG. 191. Penial anatomy of ***Torresitrachia freycineti*** n. sp. paratype AM C471781 (D'Arcy Island, June). Scale bar = 3 mm.

WAM S37023 (10 preserved specimens), WAM S37284 (38 shells), WAM S37285 (10 shells), WAM S37024 (5 preserved specimens), WAM S37286 (9 shells), WAM S37287 (3 shells), WAM S37025 (preserved specimen), WAM S37288 (4 shells), WAM S37088 (5 preserved specimens), WAM S37089 (preserved specimen), WAM S37290 (3 shells).

Etymology

In honour of Louis de Freycinet, who in 1817 led a large scientific expedition to Western Australia on board the *Uranie*; noun in genitive case.

Description

Shell (Figs. 161K–L, 189A–D): Moderate in size (D = 12.0–16.5 mm; Table 10), discoidal to very broadly conical with almost flat to weakly elevated spire; umbilicus ~ 3 mm wide; colour yellowish-brown. Protoconch ~ 2.9 mm in diameter, comprising about one whorl, with well-developed radial pustulation. Teleoconch with fine, regularly and narrowly spaced radial ribs; inner umbilical whorls covered with fine periostracal pustules; pustules directly underneath suture. Apertural lip sharp, weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Digestive anatomy (Fig. 189E–G): Jaw consisting of many plates. Radula C + 10–12 + 16–18.

Genital anatomy (Figs. 190–191): Penis rather longer than vagina, tubular with inflated distal end, straight. Epiphallus much shorter than penis, with short to moderately long, narrow epiphallic flagellum. Distal half of inner penial wall with large, roundish pustules, densely arranged in honeycomb pattern; proximal half with three to five well-developed longitudinal pilasters, two of them reaching proximal end. Inner epiphallic wall with three to

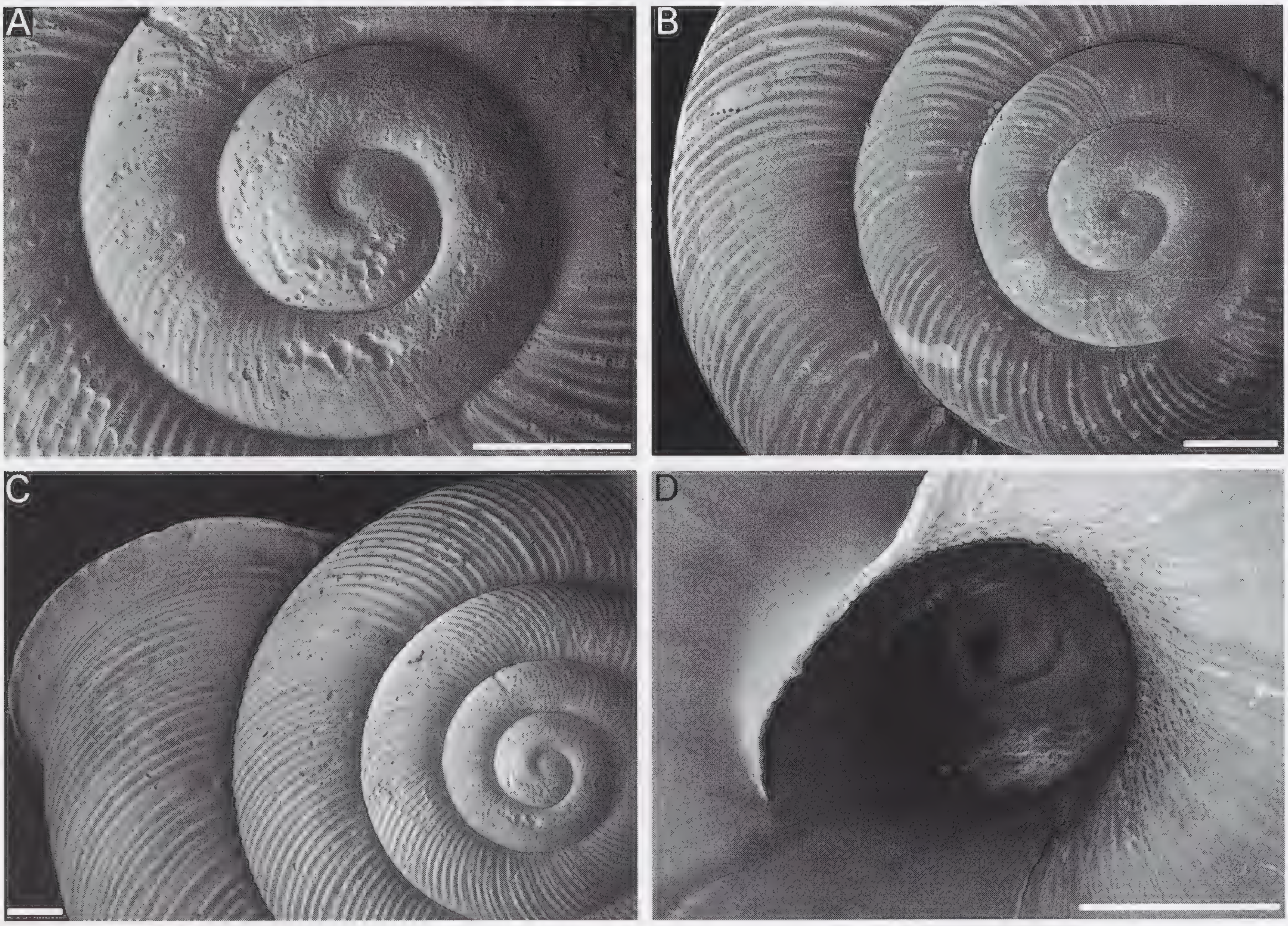

FIG. 192. SEM micrographs of the shell of ***Torresitrachia houtmani houtmani*** n. sp. & n. subsp. (unnamed island, Doubtful Bay). A–C: Paratype AM C471805. A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last and penultimate whorls; D: Paratype AM C471807 (juvenile shell), umbilicus. Scale bars = 1 mm.

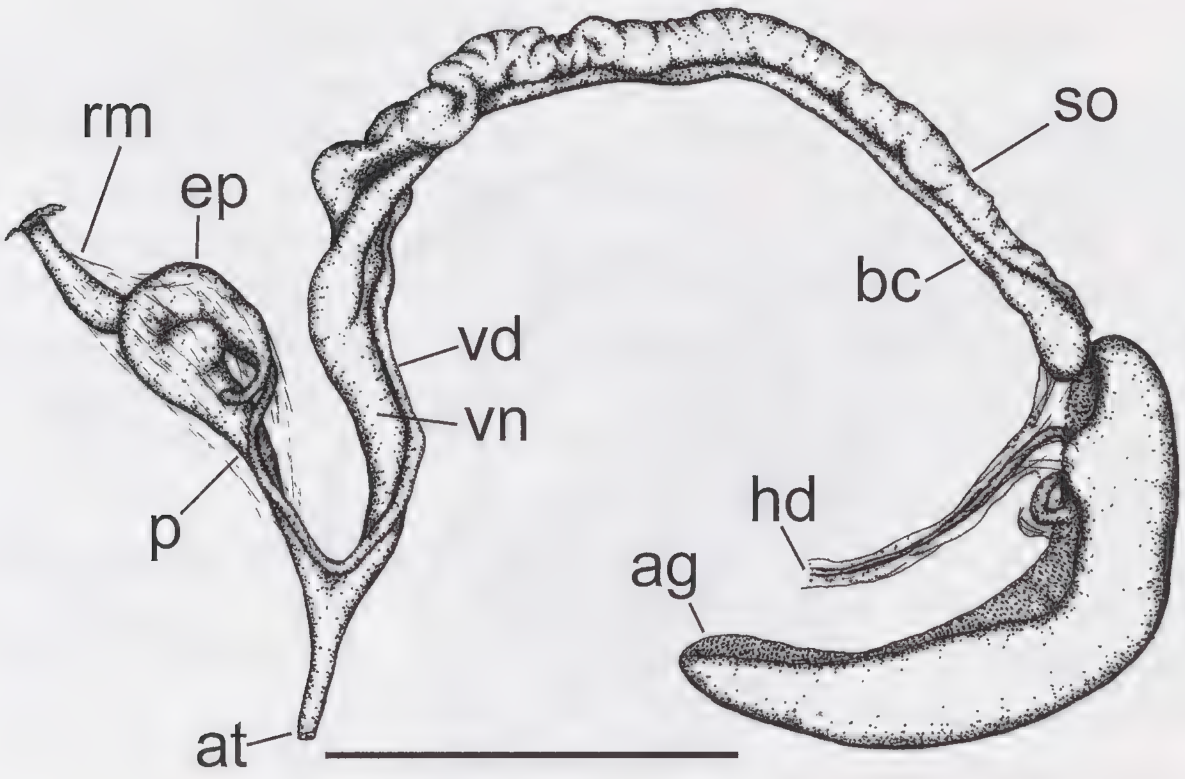

FIG. 193. Genital anatomy of ***Torresitrachia houtmani houtmani*** n. sp. & n. subsp. paratype AM C471801 (unnamed island, Doubtful Bay, May). Scale bar = 5 mm.

four well-developed longitudinal pilasters. Penial retractor muscle moderately long. Vagina about same length as free oviduct, tubular. Free oviduct moderately long, rather straight. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.001–0.008; interspecific genetic distances: 0.107–0.140 with respect to ***T. allouarni***, ***T. aquilonia***, ***T. flindersi***, ***T. girgarinae***, ***T. leichhardti*** and ***T. tasmani***; 0.204–0.228 to all other congeners.

Comparative Remarks

Closely related with species from Augustus and Byam Martin islands as judged by relatively low genetic distances. Typical features are comparatively long penis, crowded, large pustules and thick pilasters of penial wall plus thick pilasters of epiphallic wall.

Distribution

D'Arcy Island.

Torresitrachia houtmani houtmani
n. sp. & n. subsp.
Figs. 161M, 192–194

Two similar morphs were found in the Collier Bay area, one each on unnamed island, Doubtful Bay as well as Kingfisher Island, Wood Islands. These forms widely correspond in shell and genital anatomy showing only subtle but consistent differentiation with regard to shell and anatomy of inner penial wall. Preliminary analyses of mitochondrial sequences revealed forms to be mutually monophyletic with relatively low genetic distances of ~ 2%. Consistency of differences and mutual monophyly of the two forms suggests that both represent independent evolutionary entities. However, low rates of differentiation imply that reproductive incompatibility might be incomplete. From a taxonomical point of view, treatment of two allopatric forms as geographical races of a single species is considered the best way to reflect their potentially transitional nature as biological species *sensu* Mayr (1942, 1963).

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, unnamed island in Doubtful Bay, 15°54'26"S, 124°28'00"E, coll. Vince Kessner, 29/05/2009, KIS 3–159 (dry woodland on sandstone, in piles of rocks; free sealer).

Material Examined

Holotype WM S58463 (preserved specimen, Fig. 161M). Paratypes WAM S37765 (16 preserved specimens), AM C471801 (6 preserved specimens), WAM S37879 (18 shells), AM C471802 (10 shells), WAM S37758 (16 shells), WAM S37758 (4 preserved specimens), WAM S37872 (10 shells), AM C471803 (8 shells),

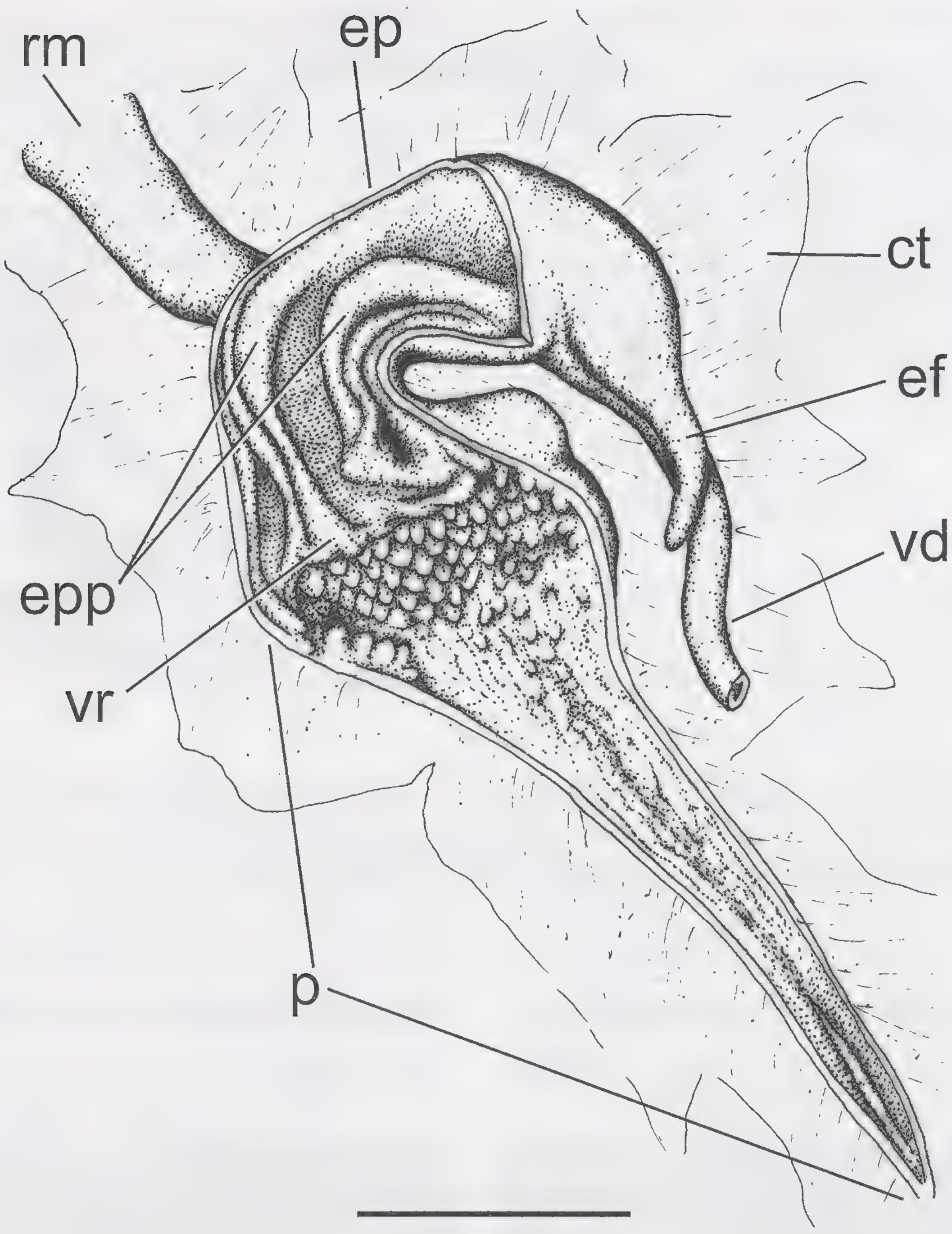

FIG. 194. Penial anatomy of ***Torresitrachia houtmani houtmani*** n. sp. & n. subsp. paratype AM C471801 (unnamed island, Doubtful Bay, May). Scale bar = 1 mm.

WAM S37759 (shell), WAM S37873 (2 shells), WAM S37760 (5 preserved specimens), WAM S37814 (14 shells), AM C471804 (10 shells), WAM S37761 (4 preserved specimens), WAM S37875 (12 shells), AM C471805 (7 shells), WAM S37876 (preserved specimen), WAM S37762 (3 preserved specimens), WAM S37877 (7 shells), WAM S37763 (shell), WAM S37764 (12 preserved specimens), AM C471806 (6 preserved specimens), WAM S37878 (10 shells), AM C471807 (5 shells), WAM S37766 (preserved specimen), WAM S37880 (3 shells), WAM S37881 (10 shells), WAM S37777 (2 preserved specimens), WAM S37882 (7 shells), WAM S37778 (preserved specimen), WAM S37883 (4 shells) all from type locality or very close by on unnamed island, Doubtful Bay.

Etymology

Named in honour of Frederick de Houtman who landed on the Western Australian shore in 1619; noun in genitive case.

Description

Shell (Figs. 161M, 192): Moderate to large in size (D = 13.9–18.0 mm; Table 10), broadly conical with moderately elevated spire; umbilicus ~ 2.3 mm wide, not or partly concealed; colour light yellowish-brown, glossy. Protoconch ~ 2.2 mm in diameter, comprising about one whorl, essentially smooth with erosion scars. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct on base of shell; inner umbilical whorls covered with fine periostracal pustules. Apertural lip sharp, weakly to well expanded, weakly reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 193–194): Penis short and thin (shorter than vagina), with inflated distal end, straight. Epiphallus shorter than penis, with short epiphallic flagellum. Distal end of inner penial wall with small, roundish pustules, loosely arranged in honeycomb pattern, tapering proximally, giving rise to very indistinct, irregularly undulating, indistinct longitudinal pilasters along proximal three quarters of interior wall. Inner epiphallic wall with two pairs of narrowly attached longitudinal pilasters. Penial complex completely embedded in thick layer of connective tissue. Penial retractor muscle short. Vagina longer than free oviduct, tubular. Free oviduct short, S-shaped. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

Torresitrachia houtmani dampieri
n. subsp.
Figs. 161N, 195–197

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, Collier Bay, Woods Islands, Kingfisher Island, 16°05'21.8"S, 124°05'34.3"E; coll. Vince Kessner, 05/06/2009, KIS 3–173 (rocky band at beach, aestivating deep under rocks, free sealer).

Material Examined

Holotype WAM S58462 (preserved specimen, Fig. 161N). Paratypes WAM S37771 (4 preserved specimens), WAM S37861 (8 shells), AM C471796 (6 shells), WAM S37767 (5 preserved specimens), WAM S37854 (10 shells), AM C471797 (6 shells), WAM S37855 (2 shells), WAM S37856 (3 shells), WAM S37857 (7 shells), WAM S37768 (2 preserved specimens), WAM S37858 (11 shells), WAM S37769 (2 preserved specimens), WAM S37859 (14 shells), AM C471798 (10 shells), WAM S37770 (7 preserved specimens), WAM S37860 (22 shells), AM C471799 (10 shells) from type locality or very close by.

Etymology

Named in honour of William Dampier, first Englishman to land on the northwest coast of what was then called New Holland in 1688; noun in genitive case.

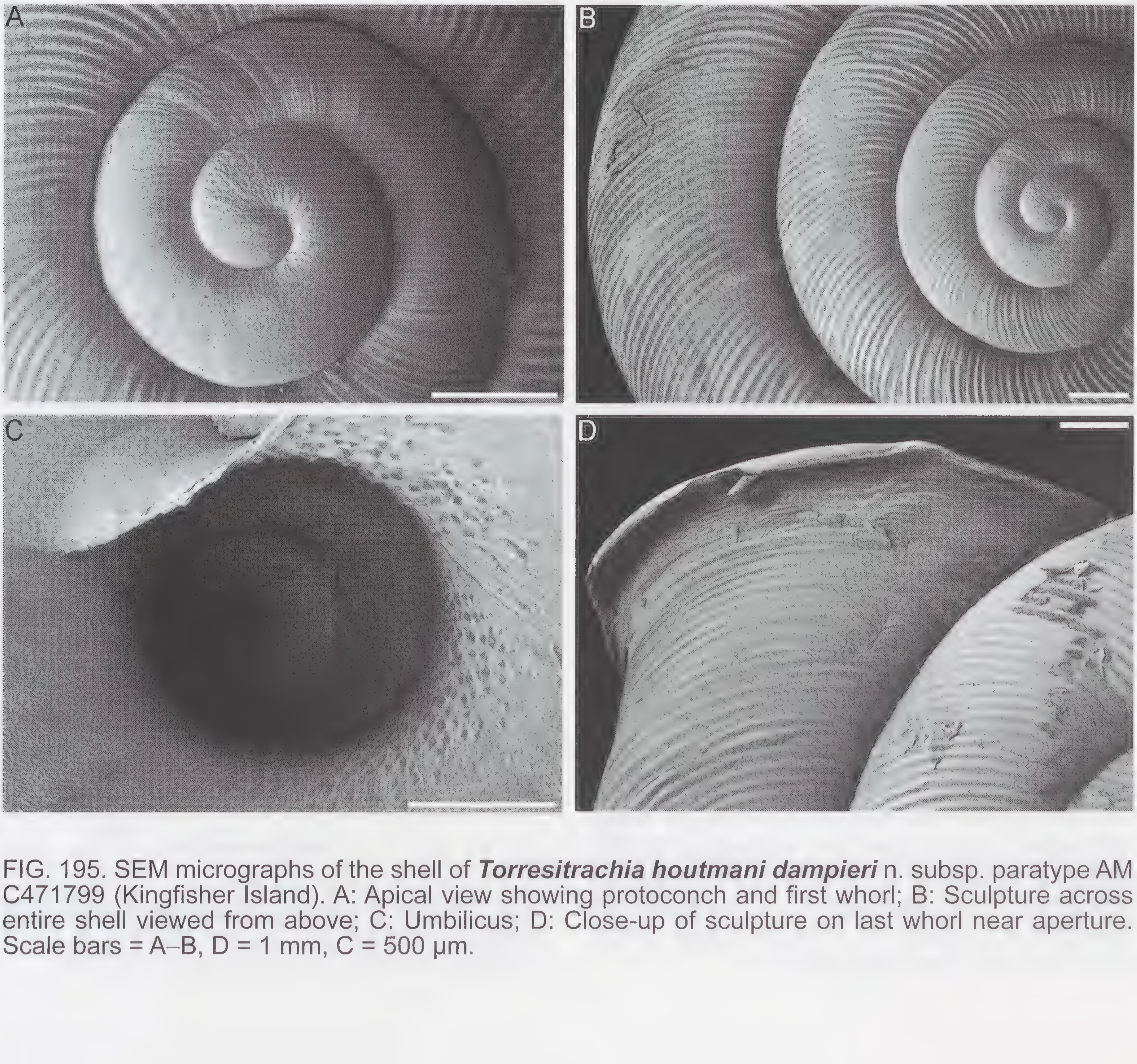

FIG. 195. SEM micrographs of the shell of ***Torresitrachia houtmani dampieri*** n. subsp. paratype AM C471799 (Kingfisher Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Umbilicus; D: Close-up of sculpture on last whorl near aperture. Scale bars = A–B, D = 1 mm, C = 500 µm.

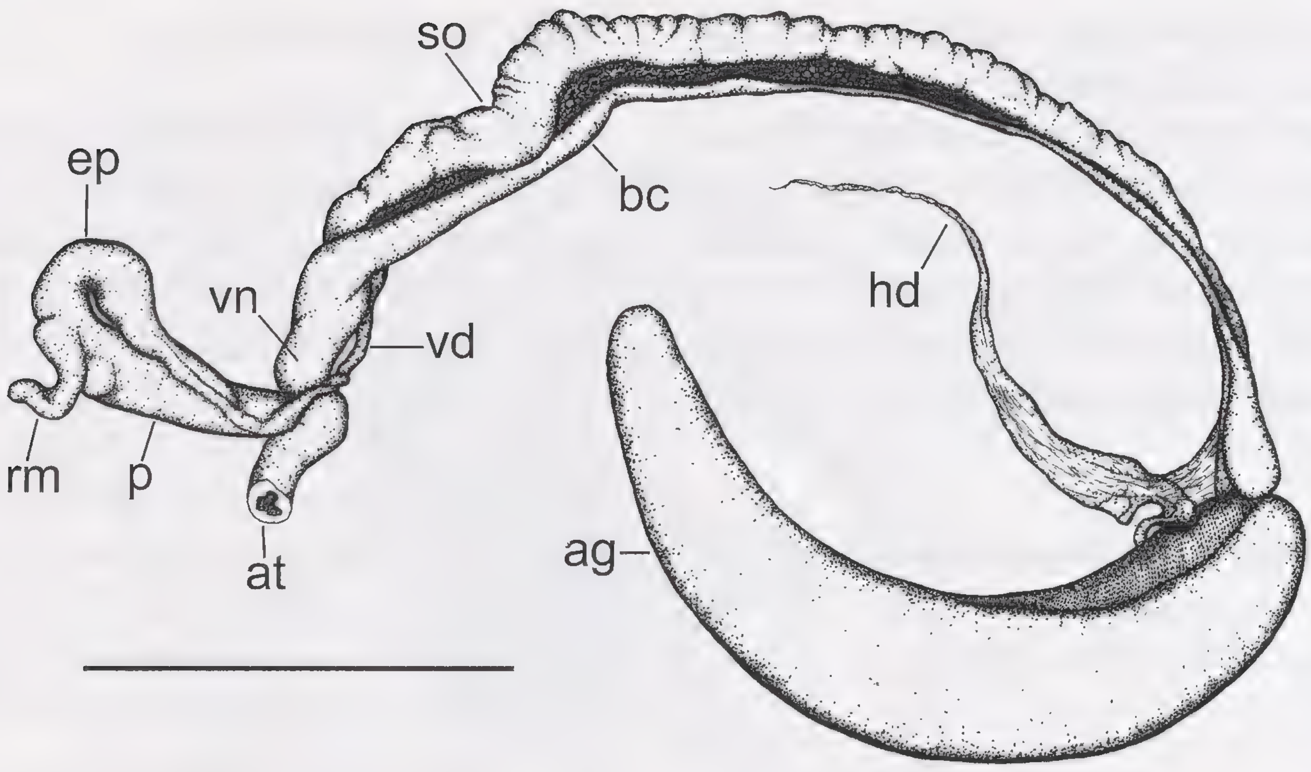

FIG. 196. Genital anatomy of ***Torresitrachia houtmani dampieri*** n. subsp. paratype WAM S37770 (Kingfisher Island, June). Scale bar = 5 mm.

Description

Shell (Figs. 161N, 197): Moderate to large in size (D = 15.8–18.8 mm; Table 10), umbilicus ~ 2.5 mm wide.

Genital anatomy (Figs. 196–197): Epiphallus slightly shorter than penis, with moderately long epiphallic flagellum. Distal end of inner penial wall with few, small rhomboid pustules, distal three quarters with four well-developed longitudinal pilasters, two of which reach proximal end. Vagina about same length as free oviduct, tubular.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.001–0.003 among nominate form, 0.019–0.021 with respect to ***T. houtmani dampieri*** (2 sequences); interspecific genetic distances: 0.103–0.108 to ***T. urvillei*** (3 sequences), 0.104–0.107 to ***T. brookei*** (2 sequences), 0.0.205–0.245 to all other congeners (22 sequences, 8 species).

Comparative Remarks

Together with ***T. janszi*** and ***T. hartogi*** among the largest species of the genus. Typical features of this species are: penis embedded into strong connective tissue, which is more delicate in other species, paired epiphallic pilasters. ***Torresitrachia houtmani dampieri*** differs from nominate form by larger shell, fewer penial wall pustules of different shape, more pronounced longitudinal pilasters.

Distribution (Fig. 160)

Known from Collier Bay area; the nominate form is found on un-named island in Doubtful Bay (nominate form), and Kingfisher Island, about 40 km to the SW (***T. houtmani dampieri***).

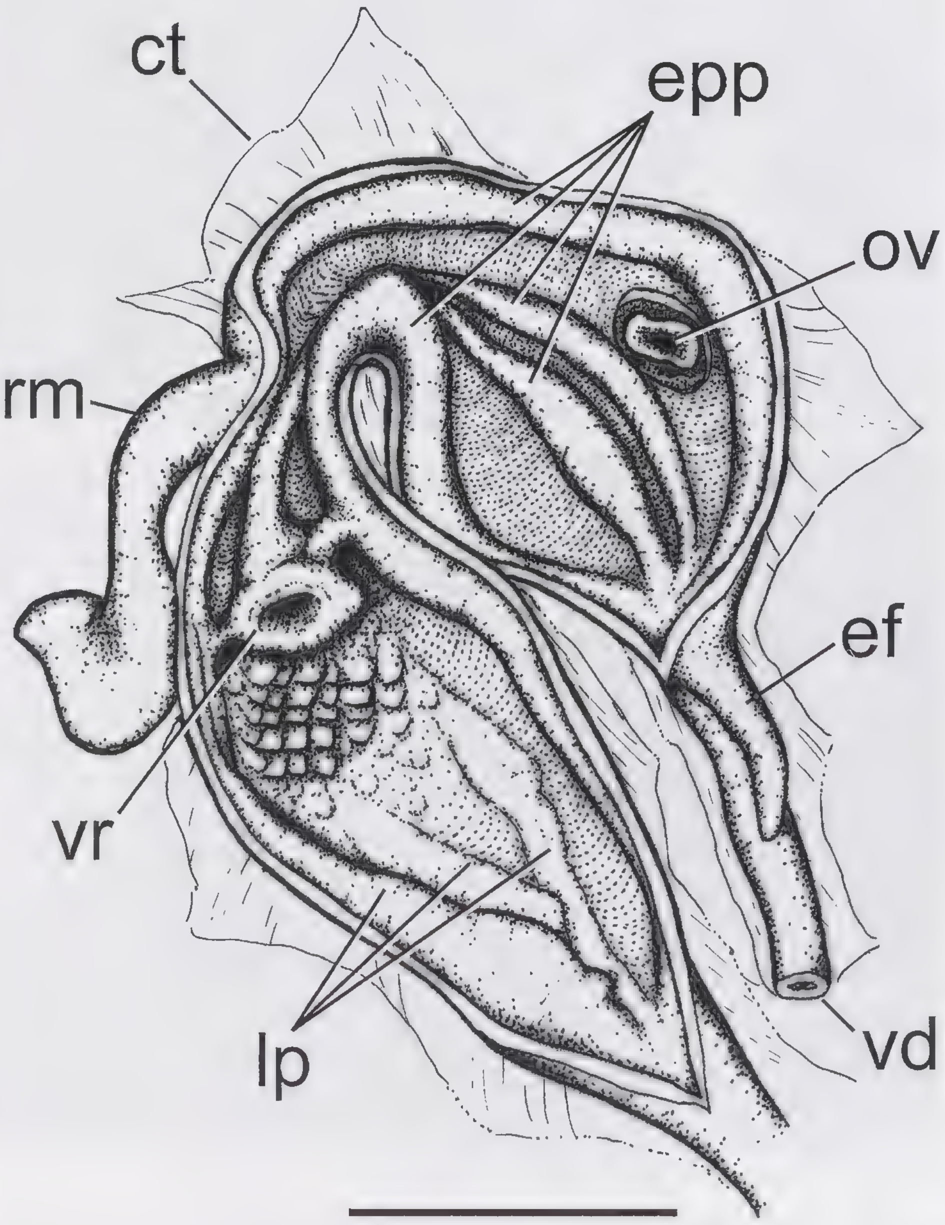

FIG. 197. Penial anatomy of ***Torresitrachia houtmani dampieri*** n. subsp. paratype WAM S37770 (Kingfisher Island, June). Scale bar = 1 mm.

Torresitrachia leichhardti n. sp.

Figs. 161O, 198–200

Type Locality

Western Australia, southwestern Kimberley, Doubtful Bay, SE section of Storr Island, 15°57'09"S, 124°33'48"E; coll. Vince Kessner, 20/05/2009, KIS 3–138 (vine thicket on lower slope, scrub in a gully; sandstone; under rocks in litter and loose soil).

Material Examined

Holotype WAM S58460 (preserved specimen, Fig. 161O). Paratypes AM C471788 (5 preserved specimens), WAM S37749 (9 preserved specimens), WAM S37844 (27 shells), AM C471789 (15 shells), WAM S37748 (10 preserved specimens), WAM S37843 (14 shells), AM C471790 (6 shells), WAM S37750 (13 preserved specimens), AM C471790 (5 preserved specimens), WAM S37845 (18 shells), AM C471791 (7 shells), WAM S37751 (3 preserved specimens), WAM S37847 (13shells), WAM S37752 (2 preserved specimens), WAM S37848 (7 shells), WAM S37753 (3 preserved specimens), WAM S37849 (8 shells), AM C471793 (4 shells), WAM S37754 (preserved specimen), WAM S37755 (preserved specimen), WAM S37850 (7 shells), WAM S37756 (preserved specimen), WAM S37852 (6 shells), WAM S37757 (2 preserved specimens), WAM S37853 (5 shells), WAM S37834 (3 shells), WAM S37772 (2 preserved specimens), WAM S37851 (5 shells), WAM S37846 (11 shells) from SE section of Storr Island.

Etymology

Named in honour of Ludwig Leichhardt (1813–1848), a German explorer and scientist who got lost in 1844 when attempting to travel inland from Brisbane to Perth; noun in genitive case.

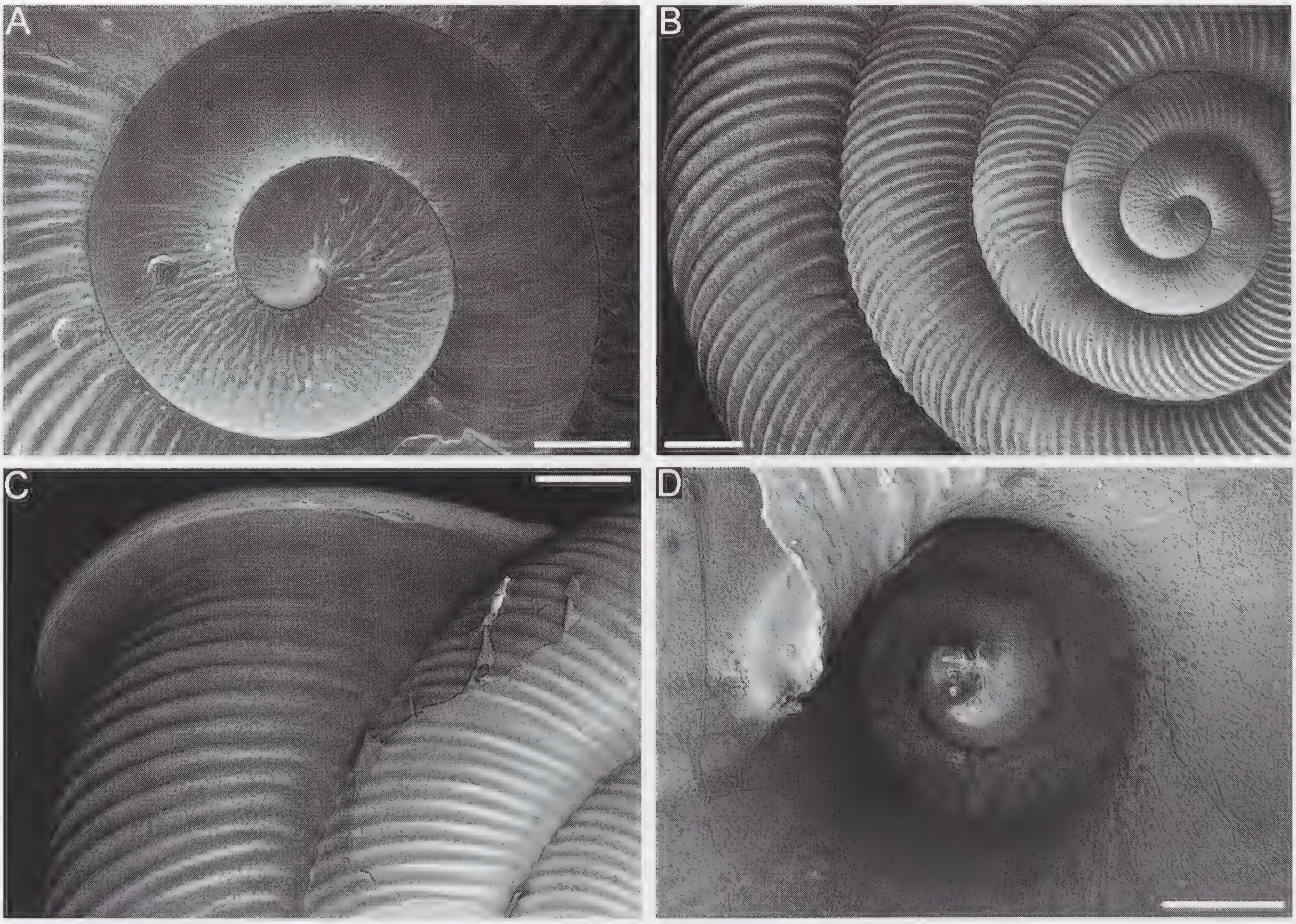

FIG. 198. SEM micrographs of the shell of ***Torresitrachia leichhardti*** n. sp. paratype AM C471789 (Storr Island). A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl near aperture; D: Umbilicus. Scale bars = A, D = 1 mm, B–C = 500 µm.

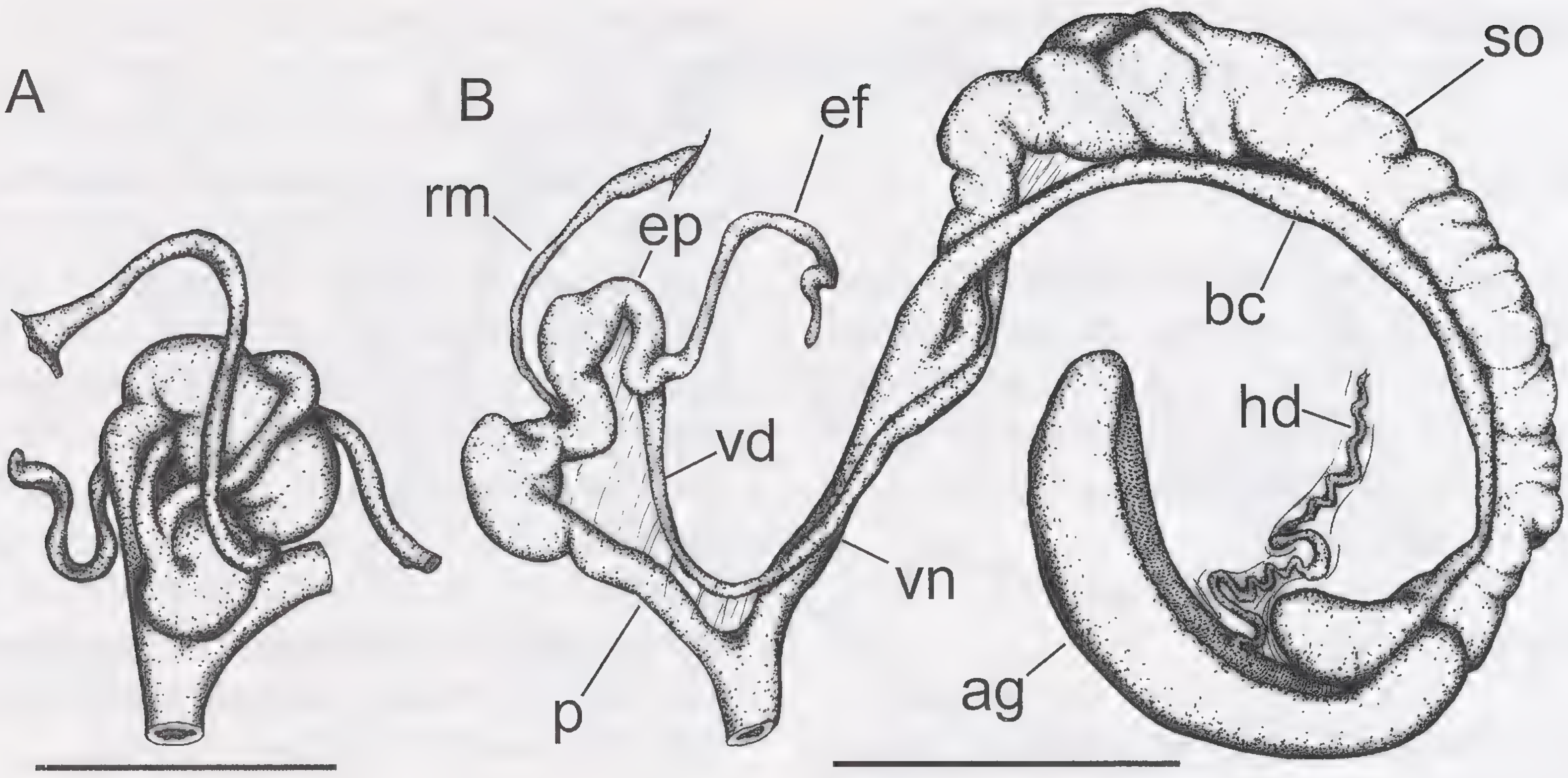

FIG. 199. Genital anatomy of ***Torresitrachia leichhardti*** n. sp. paratype AM C471791 (Storr Island, May). Scale bar = 5 mm.

Description

Shell (Figs. 161O, 198): Moderate in size (D = 12.1–15.4 mm; Table 10), discoidal to very broadly conical with almost flat to weakly elevated spire; umbilicus ~ 2.5 mm wide; colour yellowish-brown. Protoconch ~ 2.3 mm in diameter, comprising 1.5 whorls, with weak, radially arranged pustulation. Teleoconch with fine, regularly and narrowly spaced radial ribs; inner umbilical whorls covered with fine periostracal pustules. Apertural lip sharp, weakly expanded and reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 199–200): Penis short and thin (shorter than vagina), with inflated distal end, complexly coiled within thick connective tissue. Epiphallus about same length, with very long, comparatively long epiphallic flagellum. Almost entire inner penial wall covered with large, irregular, roundish pustules that give rise to irregularly undulating, well-developed longitudinal pilasters at proximal third of interior wall. Inner epiphallic wall with two to three well-developed longitudinal pilasters. Penial retractor muscle about as long as penis. Vagina comparatively long, longer than free oviduct, tubular, inner wall with longitudinal pilasters. Free oviduct short, s-shaped. Bursa copulatrix with inflated head, extending anterior end of albumen gland. Spermoviduct and albumen gland typical.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.0; interspecific genetic distances: 0.133–0.161 with respect to ***T. girgarinae***, ***T. aquilonia***, ***T. flindersi***, ***T. freycineti***, ***T. allouarni*** and ***T. tasmani***; 0.23–0.245 to all other congeners.

Comparative Remarks

Complex and tight coiling of penial complex within thick connective tissue, peculiar inner penial wall sculpture, long epiphallic flagellum and bursa copulatrix extending anterior end of albumen gland are typical features of this species.

Distribution (Fig. 160)

Known from Storr Island only.

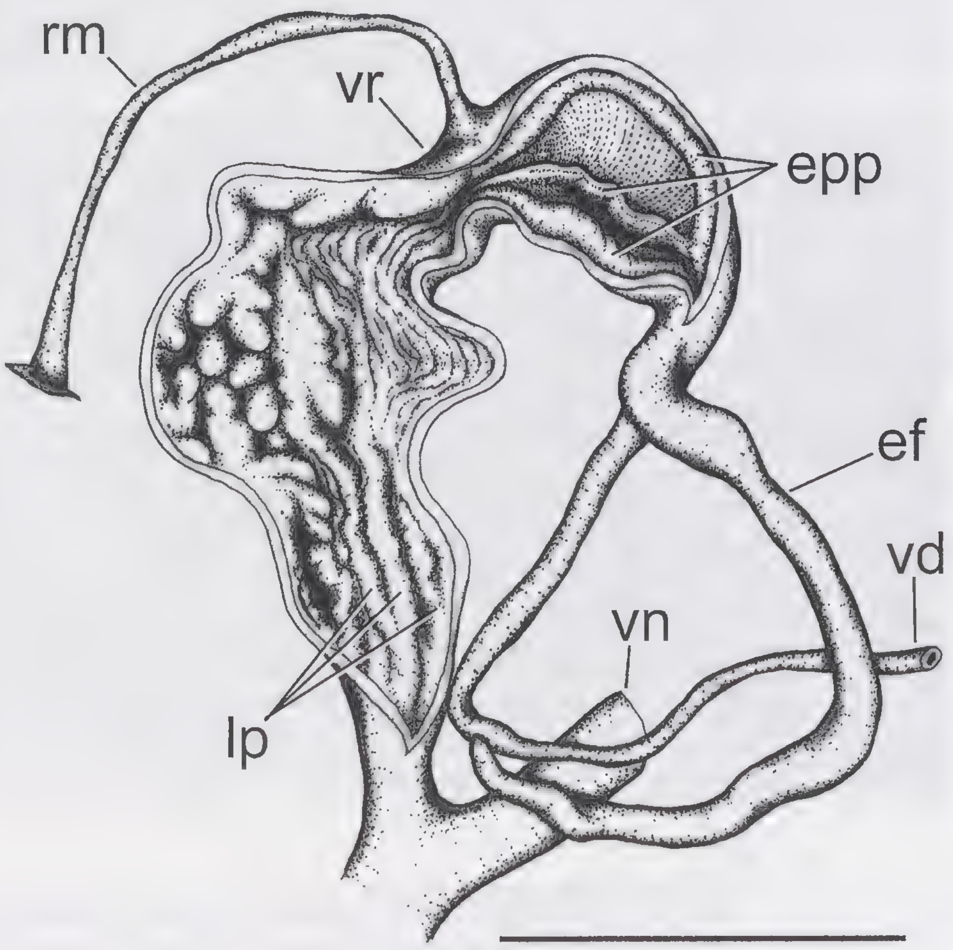

FIG. 200. Penial anatomy of ***Torresitrachia leichhardti*** n. sp. paratype AM C471791 (Storr Island, May). Scale bar = 3 mm.

Torresitrachia hartogi n. sp.
Figs. 161P, 201–203

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, Talbot Bay, N section of Molema Island, 16°15'09.7"S, 123°49'11.7"E; coll. Sean Stankowski, 27/05/2009, KIS 2–79 (rock scree in gully with vine thicket elements).

Material Examined

Holotype WAM S58461 (preserved specimen, Fig. 161P). Paratypes WAM S37742 (22 preserved specimens), AM C471794 (10 preserved specimens), WAM S37868 (8 shells), AM C471795 (4 shells), WAM S37740 (4 preserved specimens), WAM S37867 (shell), WAM S37741 (9 preserved specimens), WAM S37743 (5 preserved specimens), WAM S37744 (preserved specimen), WAM S37869 (preserved specimen), WAM S49252 (3 shells), WAM S49261 (3 preserved specimens) from northern section of Molema Island.

Etymology

Named in honour of Dirk Hartog, a Dutch explorer who in 1616 landed in Western Australia on what is now called Dirk Hartog Island; noun in genitive case.

Description

Shell (Figs. 161P, 201): Large (D = 16.8–18.5; Table 10), delicate and translucent, very broadly conical with weakly elevated spire; umbilicus ~ 2.5 mm wide; colour yellowish-brown, glossy. Protoconch ~ 3 mm in diameter, comprising about 1.5 whorls, with weak radial pustulation. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct on base of shell; inner umbilical whorls covered with fine periostracal pustules; apertural lip sharp, well expanded, weakly reflected, well

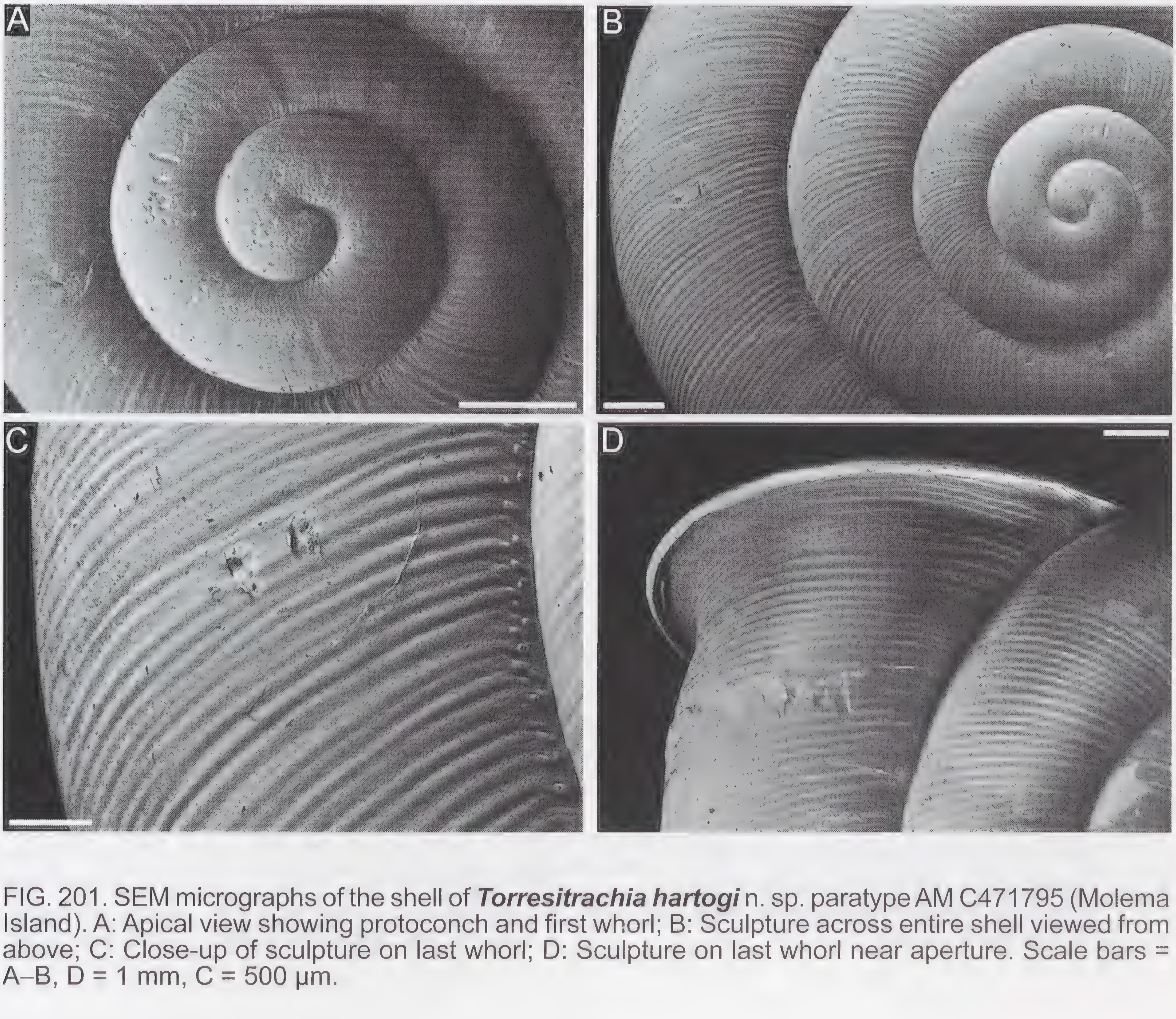

FIG. 201. SEM micrographs of the shell of ***Torresitrachia hartogi*** n. sp. paratype AM C471795 (Molema Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl; D: Sculpture on last whorl near aperture. Scale bars = A–B, D = 1 mm, C = 500 µm.

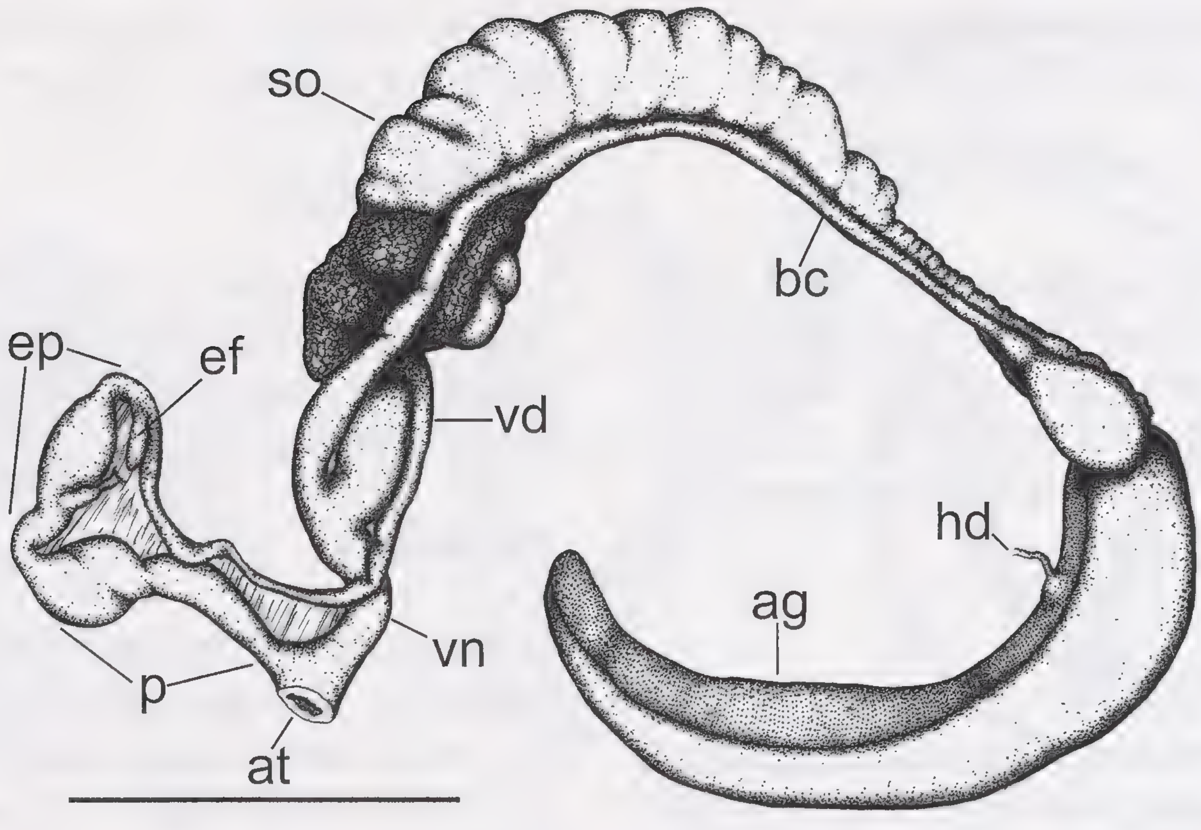

FIG. 202. Genital anatomy of ***Torresitrachia hartogi*** n. sp. paratype AM C471794 (Molema Island, May). Scale bar = 5 mm.

rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 202–203): Penis short and thin (about same length as vagina), with inflated distal end, rather straight. Epiphallus shorter than penis, with short epiphallic flagellum. Distal third of inner penial wall with large, irregular, roundish pustules, distal two thirds with three to four well-developed longitudinal pilasters. Inner epiphallic wall with well-developed longitudinal pilasters, wall in between these pilasters densely covered by minute pustules. Penial retractor muscle short. Vagina about same length as free oviduct, tubular. Free oviduct moderately long, rather straight. Bursa copulatrix with strongly inflated head, slightly extending anterior end of albumen gland.

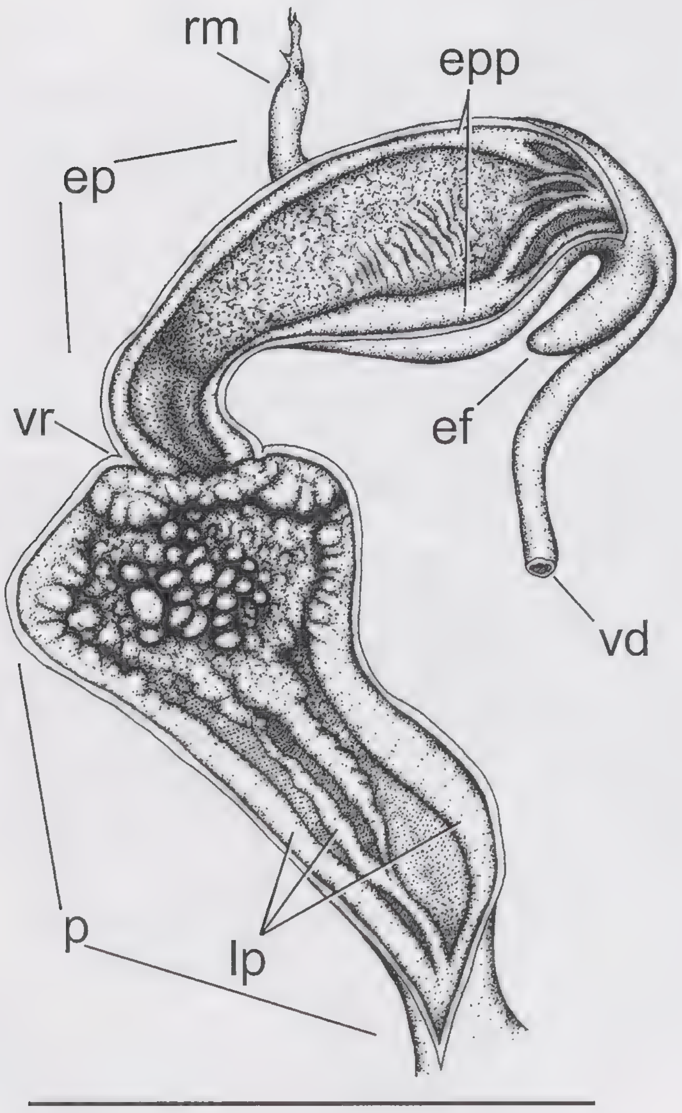

FIG. 203. Penial anatomy of ***Torresitrachia hartogi*** n. sp. paratype AM C471794 (Molema Island, May). Scale bar = 3 mm.

Mitochondrial Differentiation

Infraspecific genetic distances (3 sequences): 0.001–0.025; interspecific distances 0.059–0.066 with respect to ***T. girgarinae***, 0.106–0.152 to ***T. allouarni***, ***T. aquilonia***, ***T. baudini***, ***T. freycineti***, ***T. leichhardti*** and ***T. tasmani***; 0.199–226 to all other congeneric species.

Comparative Remarks

Very delicate, translucent and large shell is typical; axial sculpture of shell coarser than in ***T. girgarinae*** being the most closely related species as based on the low genetic distances. Characteristic features of the genital organs are irregularly sized, rounded pustules on penial wall, thick, densely covered with minute pustules in between pilasters of the epiphallic walls.

Distribution (Fig. 160)

Known from Molema Island, Talbot Bay only.

Torresitrachia girgarinae n. sp.
Figs. 161Q, 204–206

Type Locality

Western Australia, southwestern Kimberley, Buccaneer Archipelago, NW section of Hidden Island, 16°13'29.3"S, 123°26'51.4"E, coll. Sean Stankowski, 06/06/2009, KIS 2–85 (aestivating between rocks in loose soil; free sealer).

Material Examined

Holotype WAM S37747 (preserved specimen, dissected). Paratypes WAM S37745 (3 preserved specimens), WAM S37746 (preserved specimen), WAM S37871 (2 shells, Fig. 161Q), WAM S37795 (preserved specimen), WAM S37870 (shell), AM C471800 (shell) from type locality.

Etymology

For Marie Louise Victoire Girgarin, a woman who sailed disguised as male on board the ship *La Recherche* under command of D'Entrecasteaux; noun in genitive case.

Description

Shell (Figs. 161Q, 204): Small to moderate in size (D = 6.7 mm on average; Table 10), discoidal to very broadly conical with low spire; periphery rounded to weakly angulated; umbilicus ~ 2.5 mm wide; colour light yellowish-brown, glossy. Protoconch ~ 2.2 mm in diameter, comprising about one whorl, essentially smooth. Teleoconch with very fine, regularly and narrowly spaced radial ribs, becoming indistinct on base of shell; inner umbilical whorls covered with fine periostracal pustules. Apertural lip sharp, weakly to well expanded,

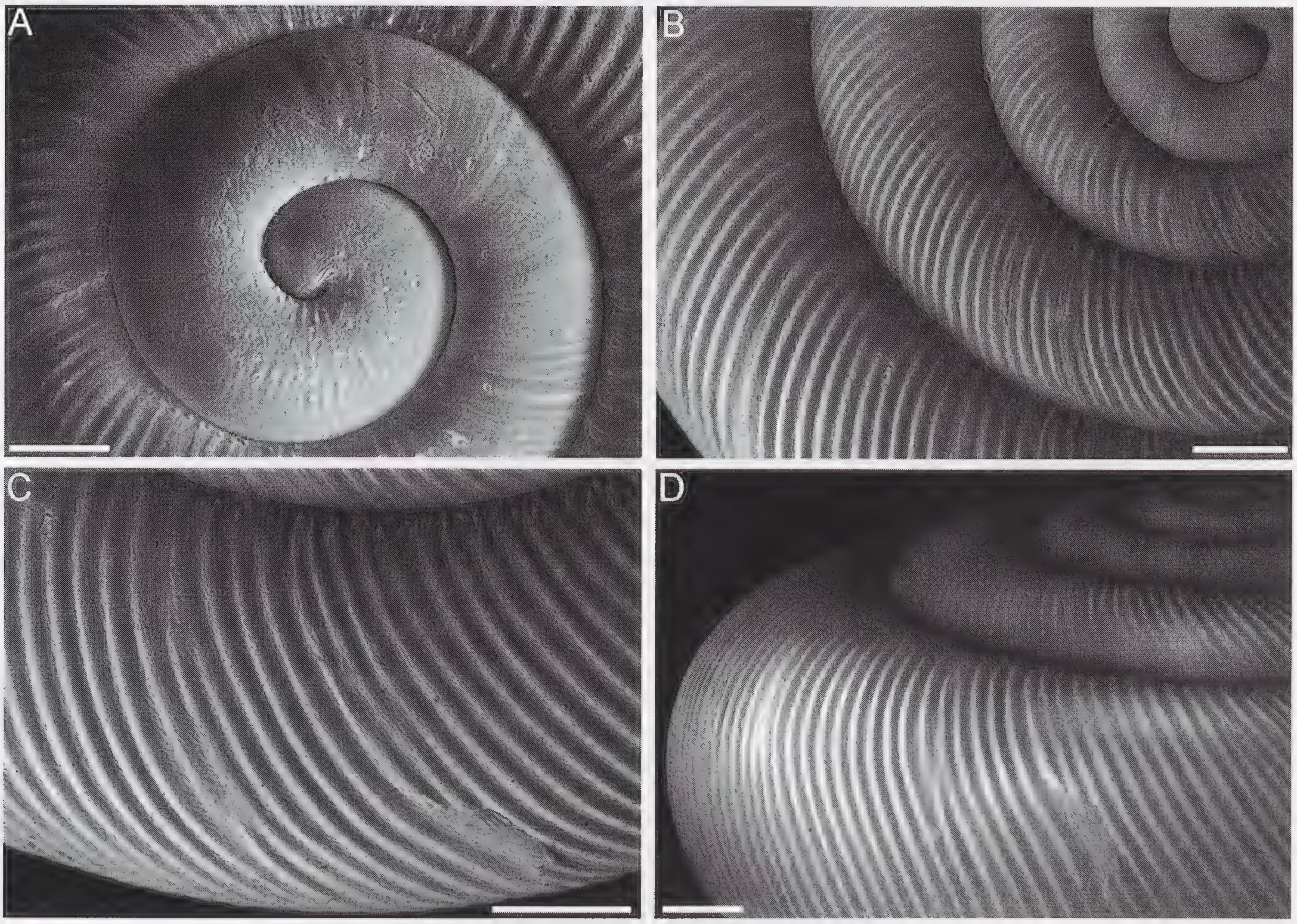

FIG. 204. SEM micrographs of the shell of ***Torresitrachia girgarinae*** n. sp. (Hidden Island). A: Holotype WAM S37747, apical view showing protoconch and first whorl. Scale bar = 500 µm; B–D: Paratype AM C471800. Scale bars = 1 mm. B: Sculpture across entire shell viewed from above; C: Close-up of sculpture on last whorl; D: Shell viewed obliquely from above, showing sculpture across whorls.

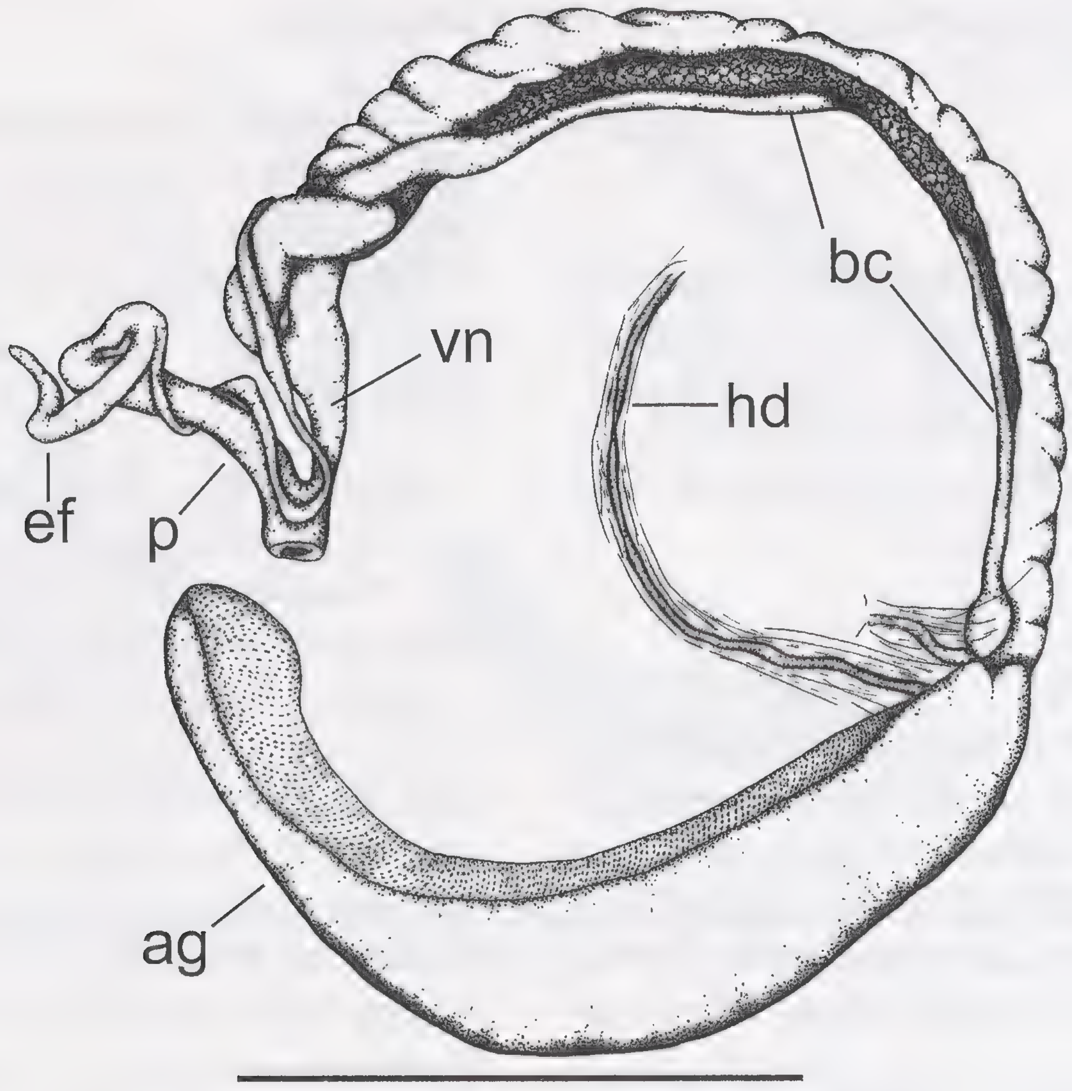

FIG. 205. Genital anatomy of ***Torresitrachia girgarinae*** n. sp. holotype WAM S37747 (Hidden Island, June). Scale bar = 5 mm.

weakly reflected, well rounded without nodes, parietal wall extremely delicate.

Genital anatomy (Figs. 205–206): Penis short, thin (about as long as vagina), rather straight. Epiphallus slightly shorter than penis, with comparatively long epiphallic flagellum. Distal third of inner penial wall with sparsely distributed, small, roundish pustules that give rise to indistinct, corrugated pilasters at proximal end. Inner epiphallic wall with two thick longitudinal pilasters, near opening to vas deferens an additional, corrugated pilaster. Penial retractor muscle short. Vagina about same length as free oviduct, tubular. Free oviduct short, coiled. Bursa copulatrix with slightly inflated head, reaching anterior end of albumen gland.

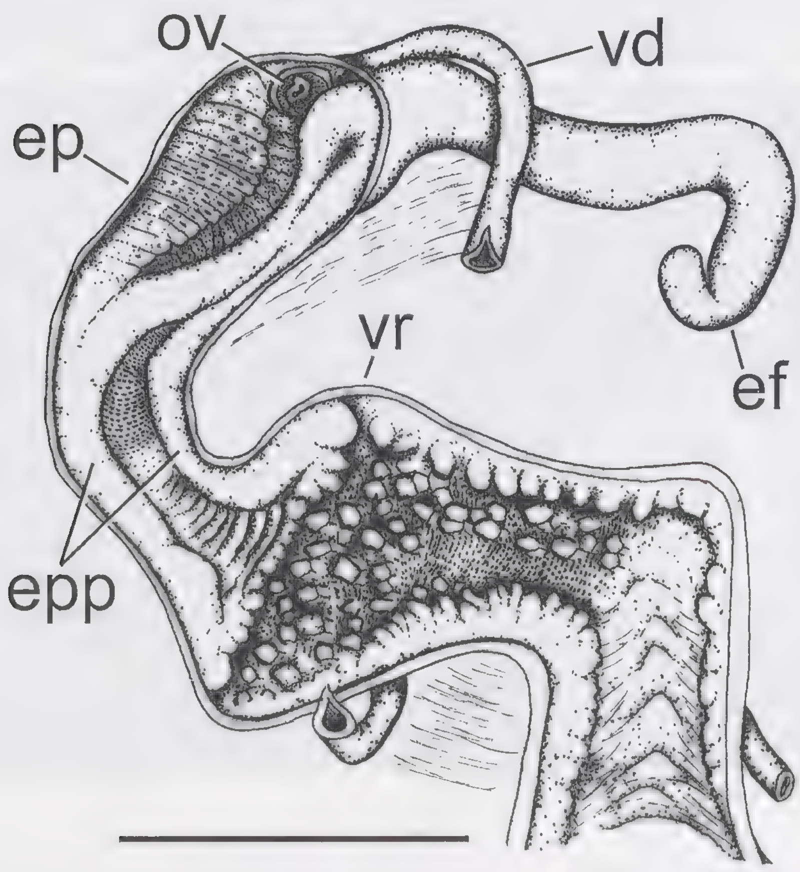

FIG. 206. Penial anatomy of ***Torresitrachia girgarinae*** n. sp. holotype WAM S37747 (Hidden Island, June). Scale bar = 1 mm.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.0–0.006; interspecific genetic distances: 0.059–0.063 with respect to ***T. hartogi***, 0.110–0.161 to ***T. aquilonia***, ***T. allouarni***, ***T. flindersi***, ***T. freycineti***, ***T. leichhardti*** and ***T. tasmani***; 0.229–0.236 to all other congeners.

Comparative Remarks

Genetically closest and most similar species is ***T. hartogi***, which differs by coarser shell sculpture, larger shell size, and details of penial and epiphallic wall sculpture.

Distribution

Buccaneer Archipelago, Hidden Island.

Kimberleytrachia n. gen.

Torresitrachia – Solem, 1979: 45–92 (partim); 1985a: 922–933 (partim); 1991: 178–185 (partim), Solem & McKenzie, 1991: 247–263 (partim).

Type species

Kimberleytrachia somniator n. sp.

Etymology

Derived from the words "Kimberley" (the region in Western Australia, where this group occurs) and the Latin word "trachea" (= windpipe, from Greek "trachea"). The suffix "–trachea" has been employed in several Australian camaenids, probably for the resemblance of radial ribs on shells with annular bands of cartilage that reinforce the windpipe of mammals. Species of the present genus lack axial ribbing but the term is employed nevertheless in continuation of the tradition to use this suffix for Australian camaenids and in distinction to "*Torresitrachia*", the name under which some of its members were previously subsumed; noun of feminine gender.

Description

Shell: Medium sized (D = 12–24 mm; Table 11), thin or mostly very delicate, discoidal to broadly conical with flat to moderately elevated spire; umbilicus narrowly open, may be partly concealed; protoconch with crowded pustules arranged in radial pattern; teleoconch lacking strongly developed radial ribs (faint radial growth lines may be present), with well-developed microsculpture of periostracal setae or projections (particularly visible in juvenile shells); whorls moderately to slowly increasing, separated by deep suture, periphery well rounded. Shell colour light to yellowish brown, no colour banding. Aperture wide, with relatively thin, weakly to moderately expanded and weakly reflected lip, palatal node absent, basal node weak or absent, parietal wall inconspicuous.

Radula: 2–5 mm long; C + 12–20 + 2–4 + 14–22.

Genital anatomy: Penis without penial sheath, embedded in connective tissue; epiphallus well developed, with well-developed epiphallic flagellum. Inner penial wall supporting simple to rather complex armature of longitudinal, oblique or transverse pilasters or lamellae, frequently with

TABLE 11. Shell parameters of ***Kimberleytrachia*** (in mm), given are maximum – minimum (mean ± standard deviation) for N measured specimens. Abbreviations used: HT = holotype.

Species	N	Height (H)	Diameter (D)	Umbilical Width	Whorls	H/D Ratio
K. somniator n. sp.	HT	13.0	22.2	2.0	4.5	0.59
	6	10.0–13.6 (12.2 ± 1.2)	18.5–22.5 (21.6 ± 1.3)	2.0–3.0 (2.5 ± 0.4)	4.1–4.8 (4.4 ± 0.2)	0.50–0.61 (0.57 ± 0.03)
K. canopi n. sp.	HT	11.8	23.6	3.5	5.2	0.50
K. alphacentauri n. sp.	HT	6.8	12.9	concealed	4.0	0.53
	17	5.6–7.5 (6.4 ± 0.5)	10.8–14.2 (12.4 ± 0.8)	concealed	3.4–4.0 (3.7 ± 0.2)	0.49–0.60 (0.52 ± 0.03)
K. chartacea n. sp.	HT	10.0	21.1	3.0	4.0	0.47
	10	9.7–11.2 (10.3 ± 0.4)	18.8–22.0 (21.0 ± 0.9)	0–3.5	4.0–4.7 (4.4 ± 0.2)	0.46–0.55 (0.49 ± 0.03)
K. amplirhagadoides n. sp.	HT	14.6	21.0	2.0	4.9	0.70
	5	12.0–14.6 (13.4 ± 0.9)	19.5–21.1 (20.4 ± 0.6)	0–2.0	4.3–4.9 (4.6 ± 0.2)	0.62–0.70 (0.65 ± 0.03)
K. achernaria n. sp.	HT	12.0	20.5	concealed	4.3	0.59
	10	11.4–13.5 (12.6 ± 0.6)	20.5–22.2 (21.4 ± 0.6)	0–2.7	4.3–4.7 (4.5 ± 0.1)	0.55–0.63 (0.59 ± 0.02)
K. crawfordi	6	12.1–13.3 (12.8 ± 0.4)	21.0–23.1 (22.0 ± 0.8)	2.7–3.2 (2.9 ± 0.2)	4.7–5.0 (4.9 ± 0.1)	0.56–0.62 (0.58 ± 0.02)

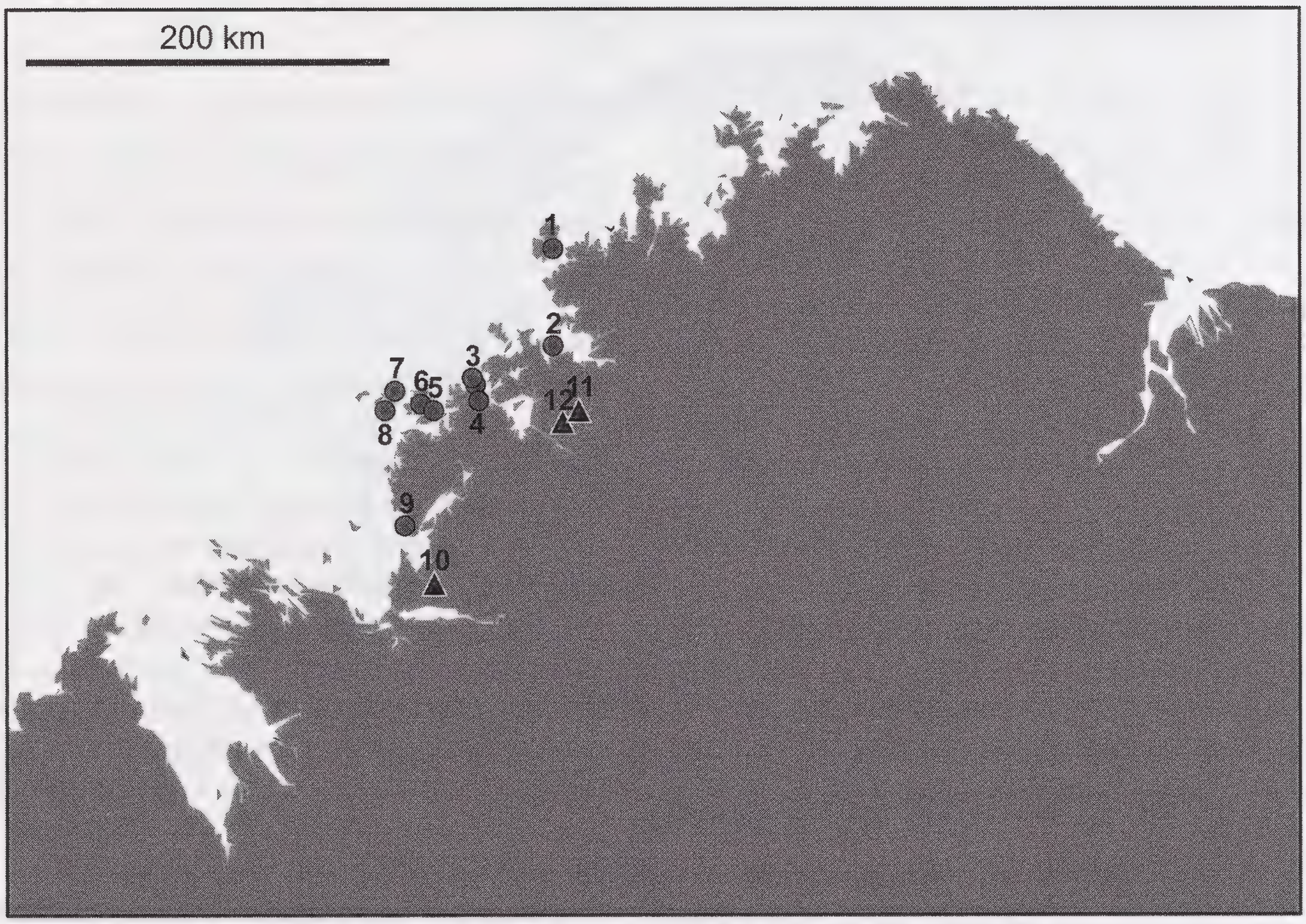

FIG. 207. Distribution map of ***Kimberleytrachia*** n. gen. Circles = records of species treated herein: 1: ***K. somniator*** n. sp. (Bigge Island), 2: ***K. alphacentauri*** n. sp., ***K. aequum*** n. sp., ***K. canopi*** n. sp. (Boongaree Island), 3: ***K. chartacea*** n. sp. (Uwins and Mictyis Islands), 4: ***K. hirsuta*** n. sp. (1.3 km S of Halfway Bay), 5: ***K. achernaria*** n. sp. (SE Augustus Island), 6: ***K. amplirhagadoides*** n. sp. (NW Augustus Island), 7: ***K. crucis*** n. sp. (D'Arcy Island), 9: *K. crawfordi* (Storr Island); triangles = records listed by Solem (1979, 1985a, 1991), 10: *K. crawfordi* (SW Doubtful Bay, N of Walcott Island), 11: *K. umbonis* (Prince Regent Reserve), 12: *K. deflecta* (Prince Regent Reserve).

pad-like swelling underneath opening to epiphallus, pustulation, lateral lamellae or more complex armature may be present. Penial retractor muscle attached at epiphallus between mid-portion to near posterior end. Epiphallus opens to penial lumen through constricting circular vergic ring. Inner epiphallic wall supporting longitudinal pilasters that vary in number and development. Vas deferens rather thin, entering epiphallus laterally near distal end or terminally through slit-like opening or often hose-like extended into lumen of epiphallus. Bursa copulatrix elongate, tubular, reaching anterior end of albumen gland.

Aestivation Strategy

Rock sealer.

Comparative Remarks

Species of this group were subsumed under the genus *Torresitrachia* for their somewhat similar shell shape and generally similar genital anatomy. However, both genera form distinct monophyla in phylogenetic trees of the Camaenidae (Köhler, 2009, 2010c). Shells of ***Kimberleytrachia*** differ by being much thinner, larger, lack of axial ribs, presence of periostracal setae (which are found in some *Torresitrachia* species as well), and more pronouncedly descending body whorl. Genitalia of ***Kimberleytrachia*** differ most conspicuously by different anatomy of inner penial wall. Species of *Torresitrachia* always exhibit a combination of distal pustulation and longitudinal pilasters in proximal part of penial wall whereas ***Kimberleytrachia*** is characterised by absence of regularly arranged, rhomboid pustules but mostly has oblique or lateral lamellae or pilasters instead. Vas deferens of *Torresitrachia* entering epiphallus terminally, while in ***Kimberleytrachia*** it enters laterally (even if often close to distal end), often as a hose-like structure. In addition, *Torresitrachia* species are free sealers while ***Kimberleytrachia*** species are rock sealers.

Based on these differentiating features, the following species are herein transferred from *Torresitrachia* to ***Kimberleytrachia***: *K. umbo-*

nis (Solem, 1979), *K. crawfordi* (Solem, 1979) and *K. deflecta* (Solem, 1985).

Diversity and Distribution (Fig. 207)

In addition to three species described by Solem (1979, 1985a) from Prince Regent Reserve and Doubtful Bay, nine species are described here from islands along the Kimberley coast between Bigge Island in the north and Doubtful Bay in the south.

Kimberleytrachia somniator n. sp.

Figs. 208A, 209–211

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, W coast of Bigge Island, base of slopes on E side of a small creek valley, south of Boomerang Bay, 14°35’00”S, 125°06’10”E; coll. Vince Kessner, 16/02/2008, KIS 1–38 (W-facing sandstone slopes, overhangs, talus; live under overhanging sandstone slab).

Material Examined

Holotype WAM S36867 (preserved specimen, dissected, Fig. 208A). Paratypes WAM S58464 (preserved specimen) from type locality; WAM S36411 (2 shells) from 14°35’16”S, 125°11’06”E; AM C471808 (shell), WAM S36412 (2 shells) from 14°35’33”S, 125°11’19”E; WAM S36413 (2 shells) from 14°35’06”S, 125°06’12”E; AM C471809 (shell), WAM S36415 (shell) from 14°35’07”S, 125°05’56”E; WAM S36416 (shell) from 14°35’12”S, 125°06’13”E; WAM S36417 (shell) from 14°34’46”S, 125°05’55”E; WAM S36758 (2 shells) from 14°35’06”S, 125°06’12”E; WAM S36970 (shell) from 14°35’32”S, 125°06’19”E.

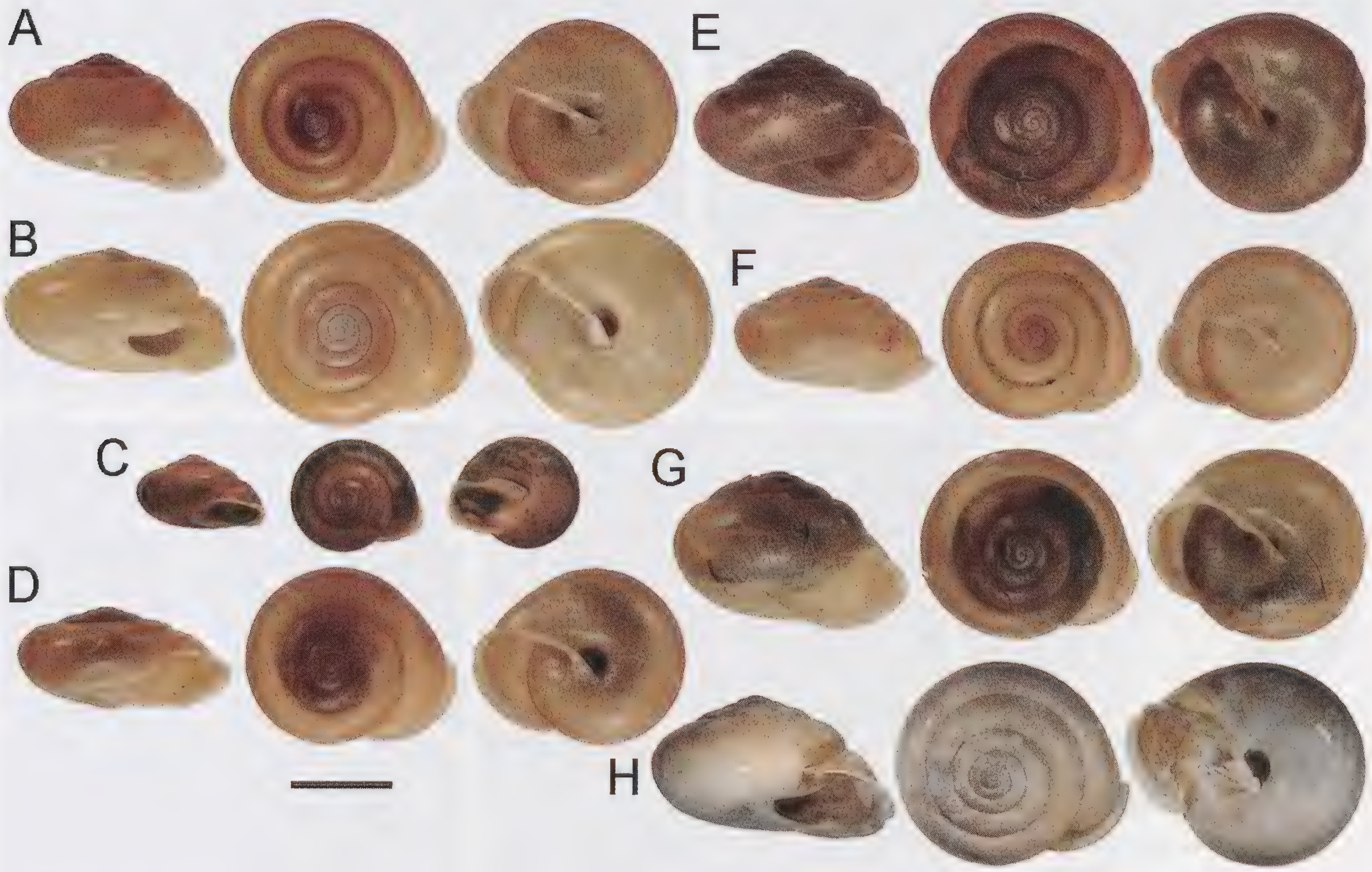

FIG. 208. Shells of ***Kimberleytrachia*** species. A: ***Kimberleytrachia somniator*** n. sp. holotype WAM S36867 (Bigge Island); B: ***Kimberleytrachia canopi*** n. sp. holotype WAM S49017 (Boongaree Island); C: ***Kimberleytrachia alphacentauri*** n. sp. holotype WAM S58465 (Boongaree Island); D: ***Kimberleytrachia chartacea*** n. sp. holotype WAM S58466 (Uwins Island); E: ***Kimberleytrachia amplirhagadoides*** n. sp. holotype WAM S58467 (Augustus Island, NW section); F: ***Kimberleytrachia achernaria*** n. sp. holotype WAM S58468 (Augustus Island, SE section); G: ***Kimberleytrachia crucis*** n. sp. holotype WAM S58469 (D’Arcy Island); H: *Kimberleytrachia crawfordi* WAM S58469 (Storr Island). Scale bar = 10 mm. Note that due to their transparency empty shells and look very different from those that contain animal; foot protrudes from shell of ***K. alphacentauri***.

Etymology

For "*somniator*" (Latin = dreamer, also a person who puts faith in dreams), referring to Dreaming as foundation of Indigenous culture and spiritual beliefs; noun in apposition.

Description

Shell (Figs. 208A, 209A–D): Moderate in size (D = 18.5–22.5 mm; Table 11), delicate, broadly conical with low or moderately elevated spire; periphery well rounded to slightly

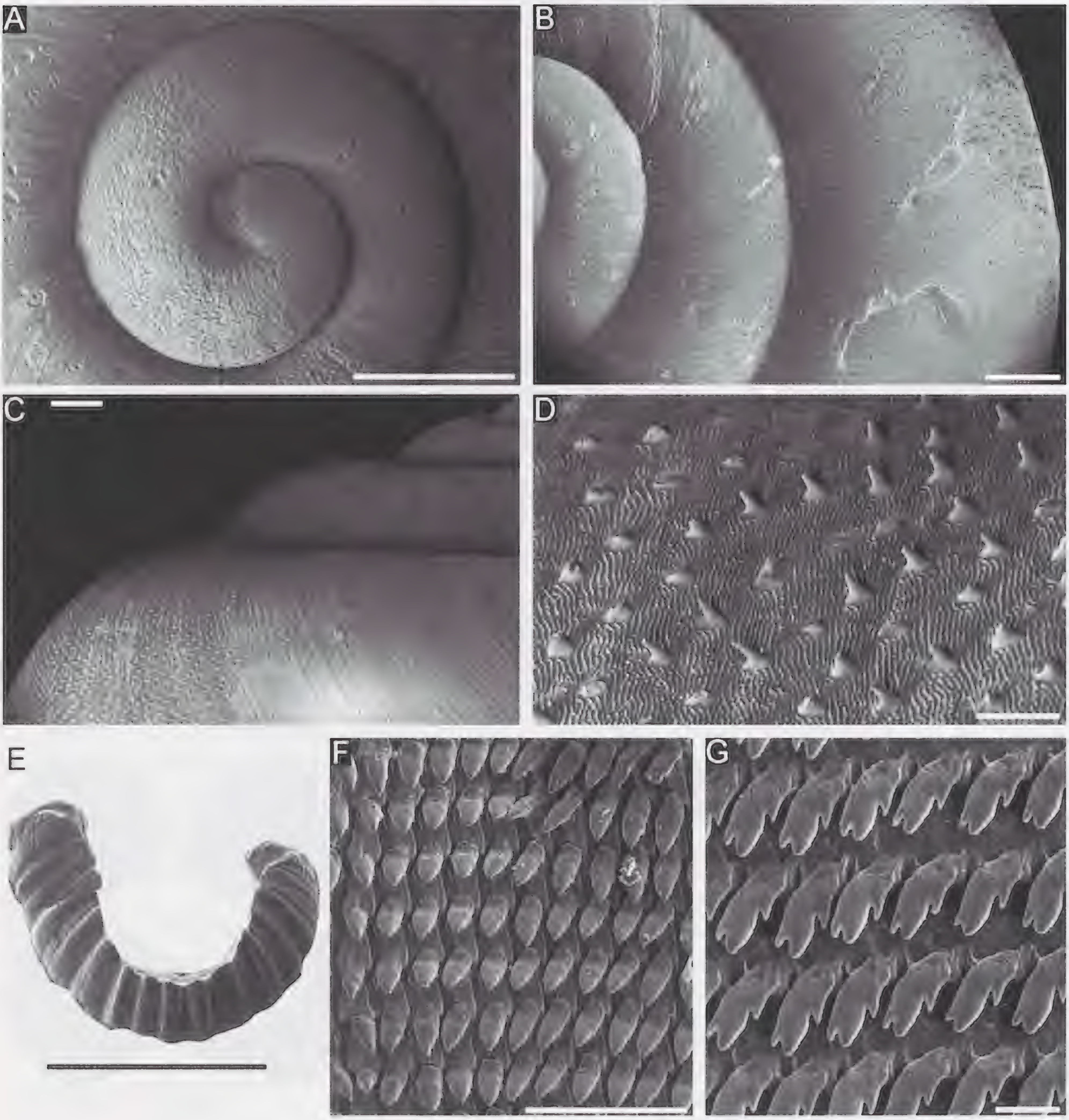

FIG. 209. SEM micrographs of ***Kimberleytrachia somniator*** n. sp. (Bigge Island). A–D: Shell paratype AM C471809. A: Apical view showing protoconch; B: Sculpture across entire shell viewed from above; C: Lateral view of last whorls. Scale bars A–C = 1 mm; D: Close-up of micro-sculpture on last whorl. Scale bar = 100 µm; E: Jaw holotype WAM S36867. Scale bar = 1 mm; F–G: Radula holotype WAM S36867. F: Central and lateral teeth viewed from above. Scale bar = 100 µm; G: Middle marginal teeth viewed obliquely from above. Scale bar = 20 µm.

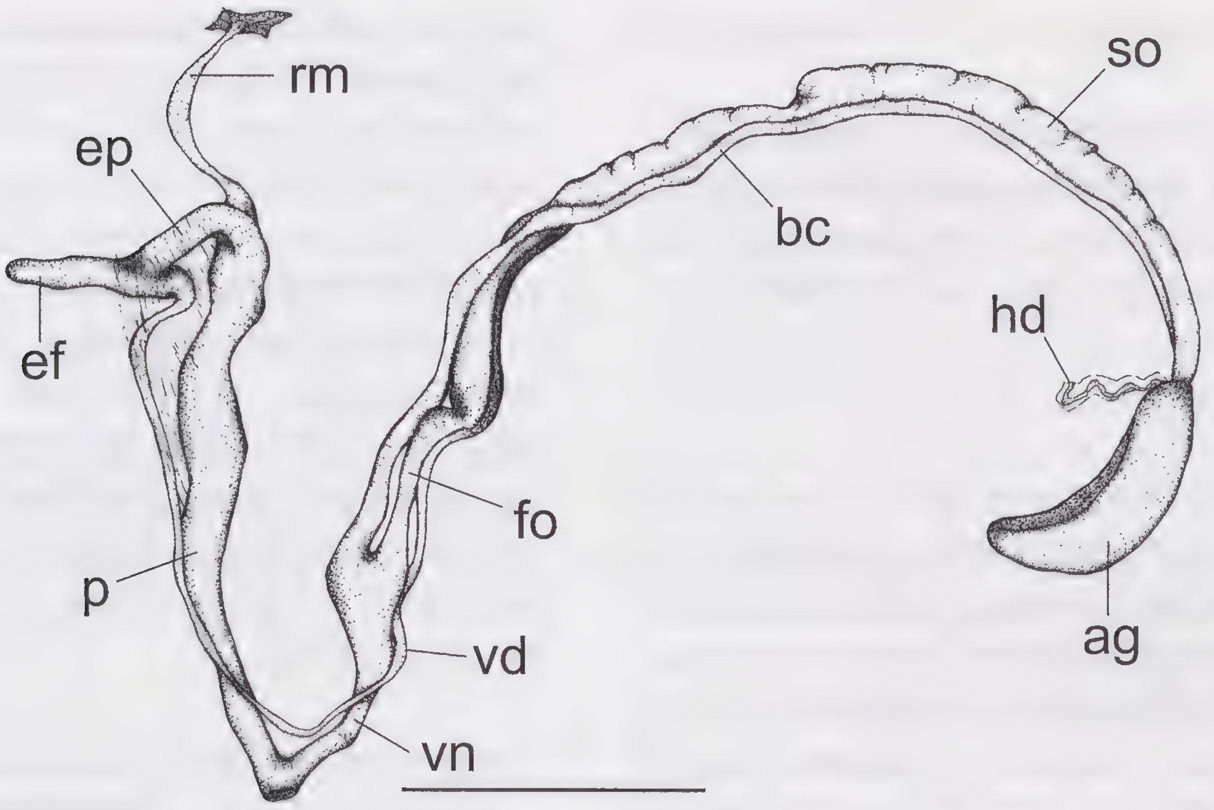

FIG. 210. Genital anatomy of ***Kimberleytrachia somniator*** n. sp. holotype WAM S36867 (Bigge Island, February). Scale bar = 5 mm.

angulated; umbilicus 1–3 mm wide, 30–90% concealed; colour amber, base of shell lighter, pale yellowish-horn. Protoconch ~ 2.4 mm in diameter, comprising 1–1.5 whorls, with very fine pustulation. Teleoconch smooth, with faint radial growth lines only; densely covered with fine periostracal setae, regularly arranged in radial pattern; microsculpture worn out in older shells giving them a glossy shine; inner umbilical whorls with well-developed pustules. Angle of aperture 30–45°; wide, simple, inside whitish, with moderately to strongly expanded, weakly reflected, thin lip; palatal node absent, basal node weakly developed.

Digestive anatomy (Fig. 211E–G): Jaw consisting of about 15 plates. Radula C + 14–16 + 3–4 + 14–18.

Genital anatomy (Figs. 210–211): Penis elongate, much longer than vagina. Inner penial wall with fine and densely packed lateral lamellae at distal end, which gradually transform into oblique pilasters at proximal end, some isolated pustules present at lateral ends of lamellae in mid-portion of inner penial wall. Epiphallus bent, attached to penis by connective tissue; much shorter than penis, with well-developed epiphallic flagellum (almost as long as epiphallus); inner epiphallic wall supporting complex of delicate longitudinal pilasters along its entire length, some of them reaching into flagellum, distal end of inner epiphallic wall supports very fine lateral lamellae in continuation of armature of penial wall. Penial retractor muscle moderately long. Vas deferens rather thin. Vagina shorter than free oviduct.

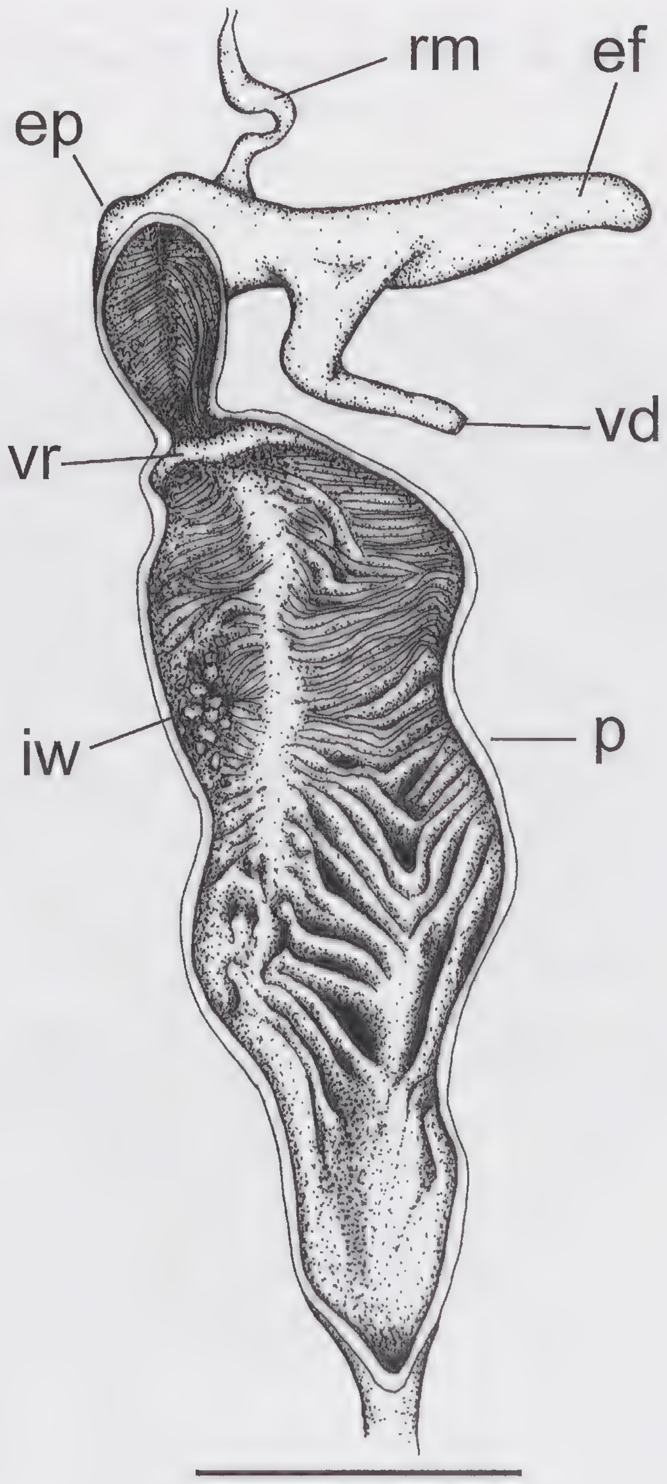

FIG. 211. Penial anatomy of ***Kimberleytrachia somniator*** n. sp. holotype WAM S36867 (Bigge Island, February). Scale bar = 2 mm.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.070–0.075 to ***K. chartacea*** (5 sequences), 0.272 to *K. crawfordi* from Storr Island, 0.093–0.105 to all other congeneric sequences.

Comparative Remarks

Shell similar to *K. umbonis* from Prince Regent Reserve; which differs most conspicuously by inner penial wall sculpture of well-developed, densely packed longitudinal pilasters at proximal end of wall distally being replaced by very fine and densely and regularly spaced lateral lamellae comprising about 80% of entire length of penial wall.

Distribution (Fig. 207)

Bigge Island.

Kimberleytrachia umbonis (Solem, 1979) n. comb.

Torresitrachia umbonis Solem, 1979: 87–91, pl. 4a–d, 7a–c, figs. 17e, f, 18a.

Type Locality

Western Australia, northwestern Kimberley, Prince Regent Reserve, Enid Falls, Rufous Creek (Fig. 207).

Taxonomic Remarks

Solem (1979) introduced this name for a species from the Prince Regent Reserve. Solem (1985a) considered specimens from the Mitchell Plateau as conspecific, which was subsequently refuted by Solem (1991), who stated that these were outside of the range of this species. Solem (1991) stated that the range of *K. umbonis* extends southward into the Saint George Basin area. This claim requires confirmation by comparative study of the anatomy. Although exhibiting a similar shell, species from various islands treated below are not conspecific with *K. umbonis* as evidenced by their distinct genital anatomy. Here placed in ***Kimberleytrachia*** for exhibiting typical characteristics of shell and genitalia.

Diagnosis

Shell: Large (D = 20.4 on average), broadly conical with moderately elevated spire, slightly angulated periphery, umbilicus almost entirely concealed; teleoconch with fine, widely spaced pustules joined by weak radial ridges, radial ribs becoming more prominent on third whorl; body whorl sharply descending.

Genital anatomy: Inner penial wall sculptured with regular, dense, well-developed circular ridges, anteriorly gradually dissolving into longitudinal pilasters. Epiphallus shorter than penis, with short flagellum; inner epiphallic wall with longitudinal pilasters (adapted from Solem, 1979).

Kimberleytrachia deflecta (Solem, 1985) n. comb.

Torresitrachia deflecta Solem, 1985a: 925–930, pl. 93a–d, 94a–e, figs. 236a–c, 237a–c.

Type Locality

Western Australia, northwestern Kimberley, Upper Prince Regent Reserve, valley of the Youwanjela Creek (Fig. 207).

Taxonomic Remarks

Solem (1985a) introduced this name for a species from the Upper Prince Regent Reserve. Solem (1991) stated that it ranges from Prince Fredrick Harbour in the north to the Saint George Basin in the south, which requires confirmation by comparative study of the anatomy. Here placed in ***Kimberleytrachia*** for exhibiting typical characteristics of the inner penial wall.

Diagnosis

Shell: Small (D = 12.6 on average), broadly conical with moderately elevated spire, weakly angulated periphery, umbilicus partly concealed; teleoconch with fine, widely spaced, radially elongated ridglets plus microsculpture of fine periostracal ridglets; body whorl sharply descending.

Genital anatomy: Inner penial with complex sculpture of intersecting longitudinal pilasters on anterior two thirds giving rise to fishbone-pattern of V-shaped rather horizontal pilasters on distal third. Epiphallus as long as penis, with short flagellum; inner epiphallic wall with many, densely packed, delicate longitudinal pilasters (adapted from Solem, 1985a).

Kimberleytrachia canopi n. sp.

Figs. 208B, 212–214

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of Boongaree Island, 15°04'19"S, 125°11'18"E; coll. Vince Kessner, 07/02/2009, KIS 1–65 (vine thicket/rainforest on steep upper slopes, large boulders; active on trees at night after rain).

Material Examined

Holotype WAM S49017 (shell, Fig. 208B), WAM S29306 (body of the same individual).

Etymology

For the name of the brightest star in the southern constellation Carina and Nova Artis, Canopus. Until the invention of the magnetic compass, this bright star was important for navigation and served as a southern pole star, noun in genitive case.

Description

Shell (Figs. 208B, 212): Large (D = 23 mm), delicate, broadly conical with rather low spire; periphery slightly angulated, upper sector of whorls well rounded, whorls separated by deeply incised suture; umbilicus narrowly open, 3.5 mm wide, 30% concealed; colour amber, base of shell lighter, pale yellowish-horn. Protoconch ~ 2.7 mm in diameter, comprising one whorl, almost smooth. Teleoconch with well-developed radial growth lines; microsculpture of sparsely distributed periostracal setae worn in adult shells; inner umbilical whorl with some pustules. Last whorl strongly descending behind aperture; angle of aperture 30°; wide, simple, with moderately to strongly expanded, weakly reflected, thin lip; palatal node absent, basal node well developed.

Genital anatomy (Figs. 213–214): Penis elongate, about same length as vagina. Inner penial wall with well-developed longitudinal pilasters at proximal half; pilasters becoming corrugated towards distal end of wall, ultimately dissolving into complex structure of undulating lamellae

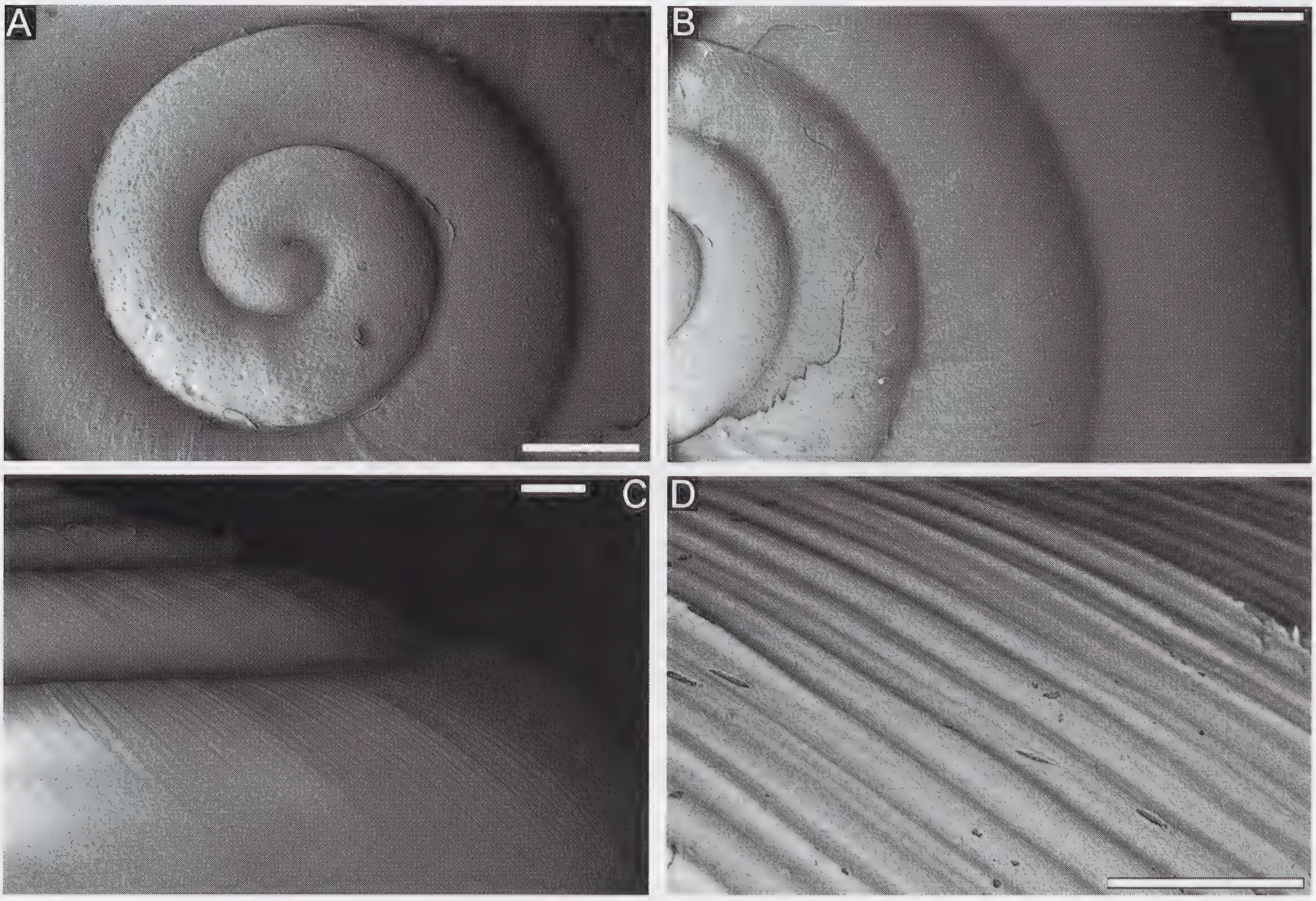

FIG. 212. SEM micrographs of the shell of ***Kimberleytrachia canopi*** n. sp. holotype WAM S49017 (Boongaree Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Lateral view of last whorls. Scale bars A–C = 1 mm; D: Close-up of microsculpture on last whorl. Scale bar = 500 µm.

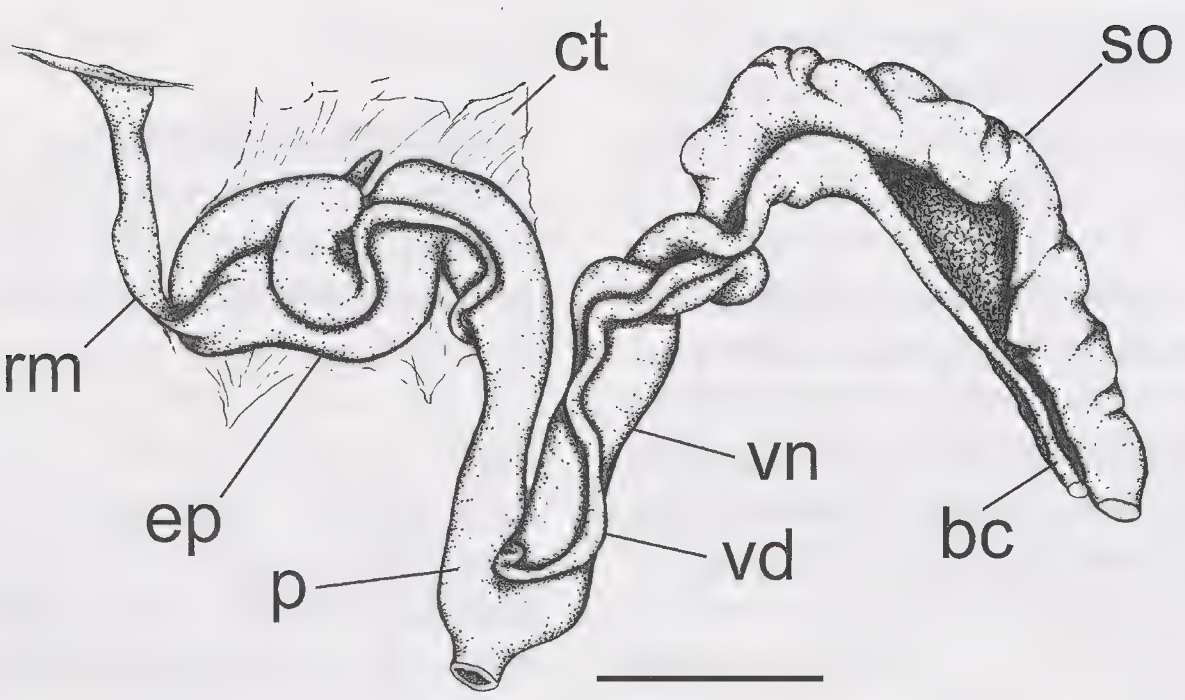

FIG. 213. Genital anatomy of ***Kimberleytrachia canopi*** n. sp. holotype WAM S29306 (Boongaree Island, February). Note that distal parts of spermoviduct, bursa copulatrix and albumen gland are lacking. Scale bar = 5 mm.

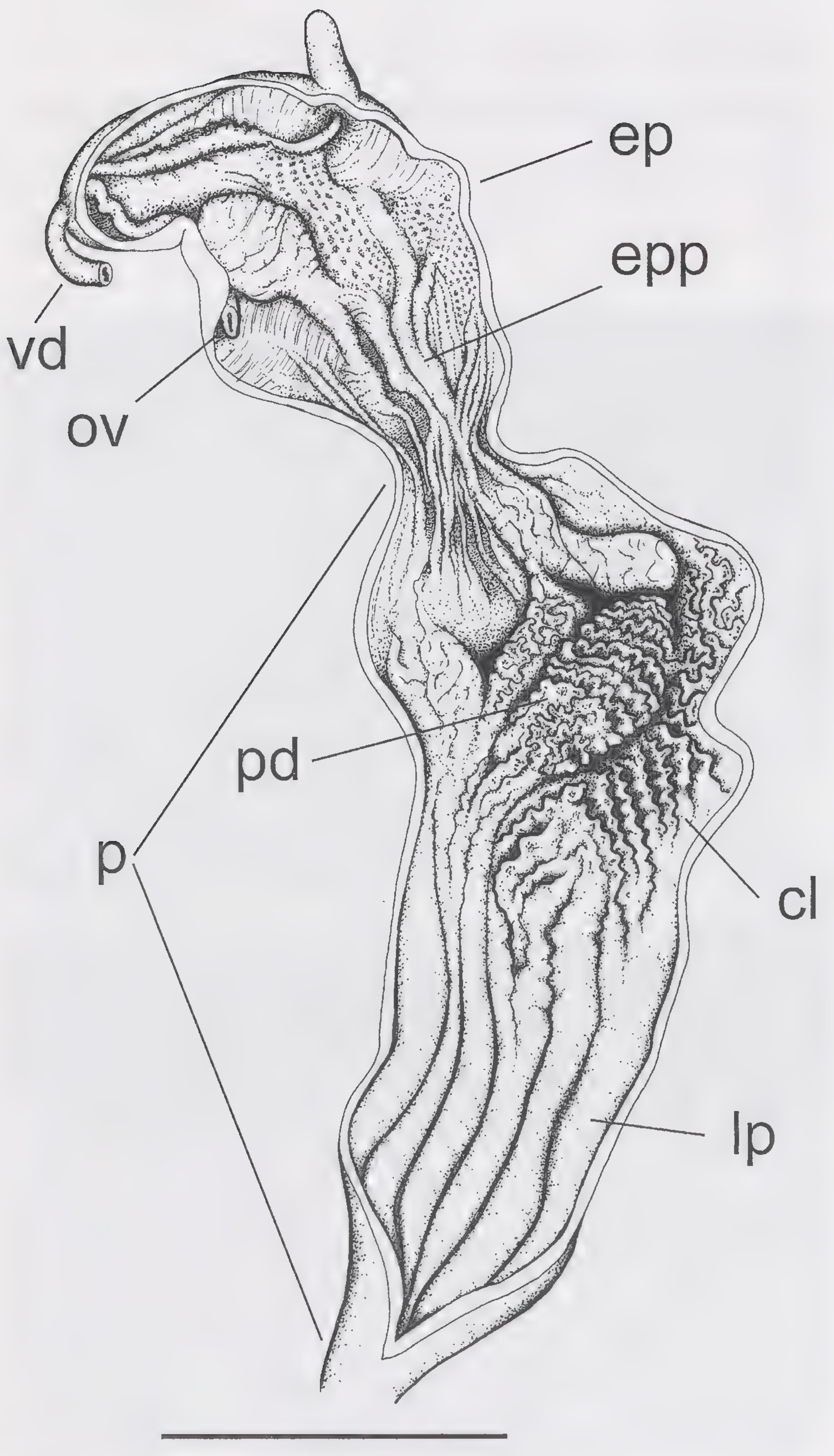

FIG. 214. Penial anatomy of ***Kimberleytrachia canopi*** n. sp. holotype WAM S29306 (Boongaree Island, February). Scale bar = 5 mm.

and partly elongated pustules that are arranged to form a pad-like elevation underneath opening to epiphallus. Epiphallus coiled, attached to penis by connective tissue; slightly shorter than penis, epiphallic flagellum short; inner epiphallic wall supporting complexly interdigitating, delicate longitudinal pilasters along entire length, some of which reaching into the flagellum; distal end of inner epiphallic wall with highly complex armature consisting of fine lamellae and net-like corrugations bound by longitudinal pilasters. Penial retractor muscle moderately long. Vas deferens entering epiphallus close to distal end, thin. Vagina much longer than free oviduct. Free oviduct coiling.

Comparative Remarks

Shell similar to *K. umbonis* and ***K. somniator*** overall, differing by slightly larger size, flatter shape, almost unconcealed umbilicus, and weakly developed periostracal microsculpture. Complex armature of inner penial and epiphallic walls is characteristic.

Distribution (Fig. 207)

Boongaree Island.

Kimberleytrachia alphacentauri n. sp.

Figs. 208C, 215–217

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, central section of

Boongaree Island, 15°04’36”S, 125°11’12”E; coll. Michael Shea, 8/08/2007, KIS 1–28 (rainforest on N-facing sandstone scree below escarpment; under rocks).

Material Examined

Holotype WAM S58465 (preserved specimen, Fig. 208C). Paratypes AM C471810

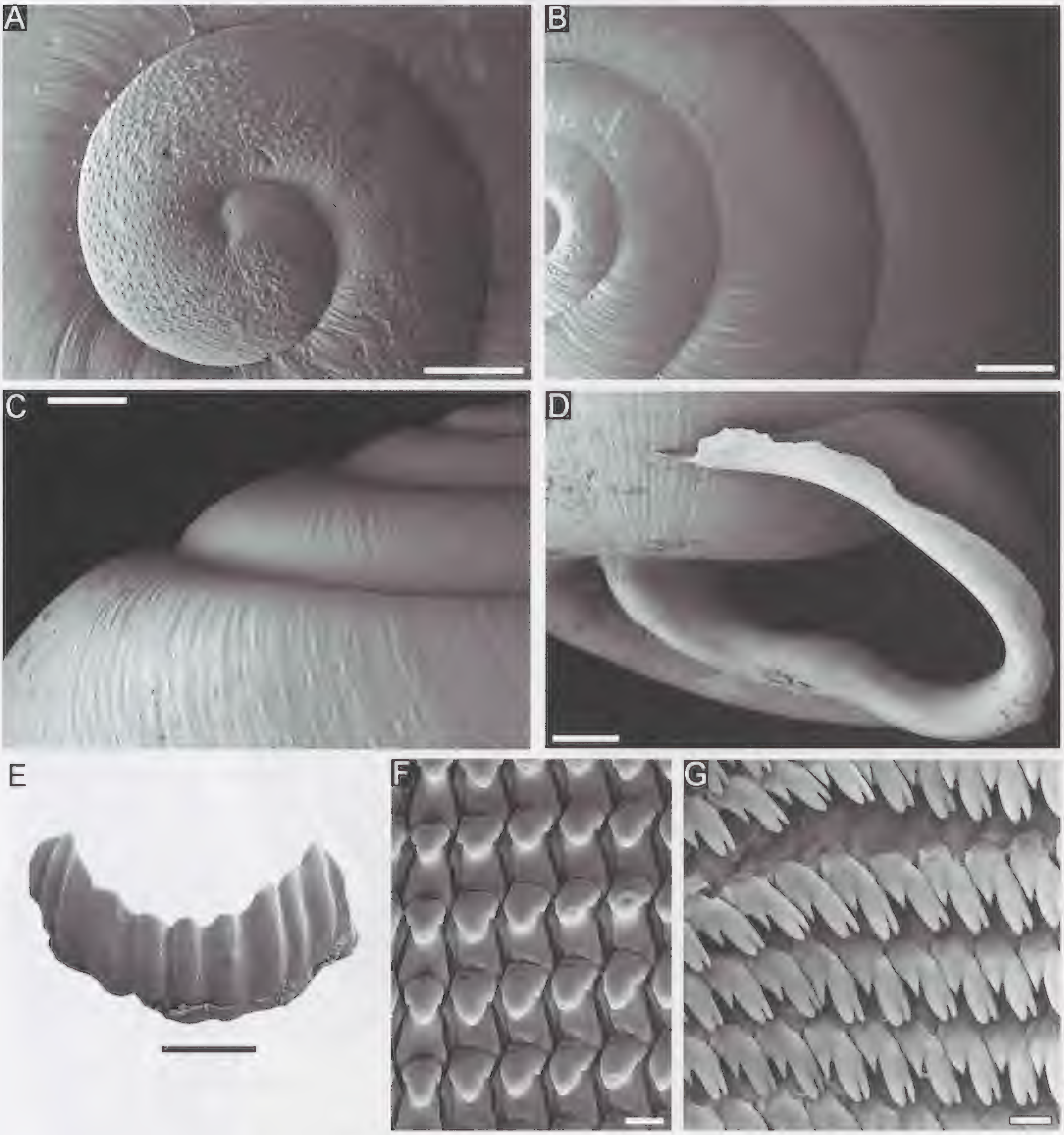

FIG. 215. SEM micrographs of ***Kimberleytrachia alphacentauri*** n. sp. (Boongaree Island). A–D: Shell paratype WAM S36403. A: Apical view showing protoconch. Scale bar = 500 µm; B: Sculpture across first whorls of shell viewed from above; C: Lateral view of last whorls showing sculpture on last whorls; D: Close-up of aperture. Scale bars = 1 mm; E: Jaw paratype AM C471810. Scale bar = 200 µm; F–G: Radula paratype AM C471810. Scale bars = 100 µm; F: Central and inner lateral teeth viewed from above; G: Middle marginal teeth viewed from above.

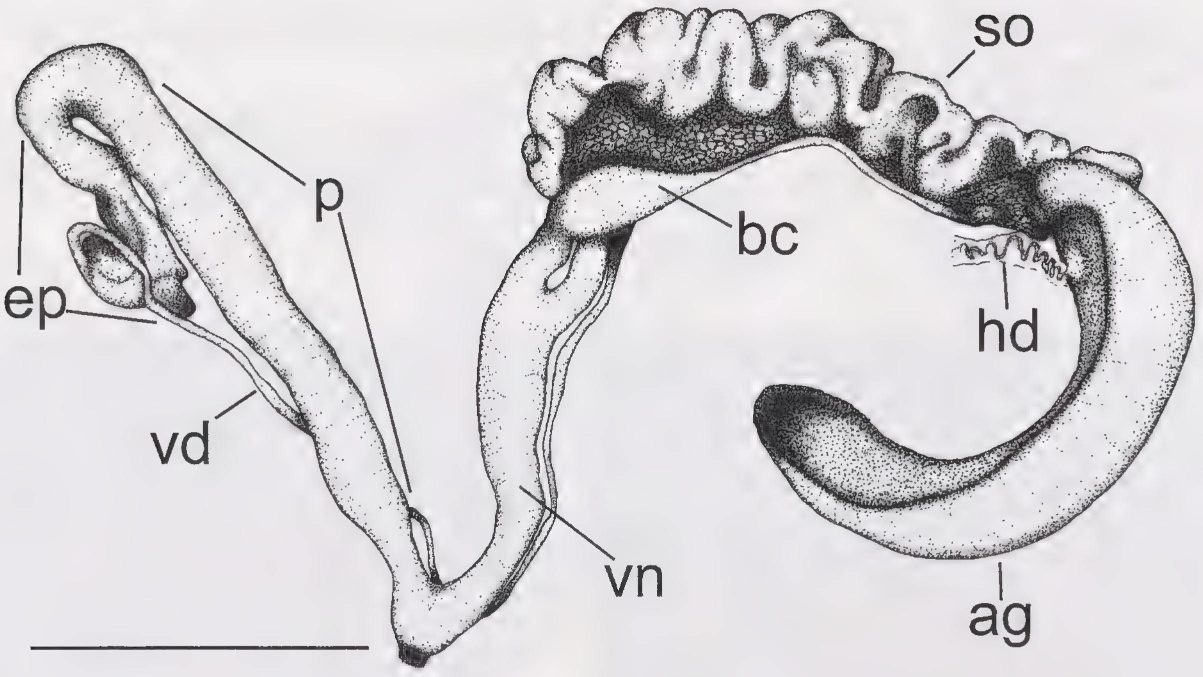

FIG. 216. Genital anatomy of ***Kimberleytrachia alphacentauri*** n. sp. paratype AM C471810 (Boongaree Island, August). Scale bar = 5 mm.

(5 preserved specimens), WAM S36740 (10 preserved specimens), AM C471811 (4 shells), WAM S36406 (6 shells) from type locality; WAM S36403 (shell) from 15°04'21"S, 125°11'06"E; WAM S36404 (shell) from 15°04'31"S, 125°11'07"E; WAM S36405 (shell) from 15°04'26"S, 125°10'46"E; WAM S36741 (9 preserved specimens), WAM S36407 (6 shells) from 15°04'15"S, 125°11'14"E; WAM S36408 (shell) from 15°04'16"S, 125°10'47"E; WAM S36402 (preserved specimen) from 15°04'00"S, 125°11'11"E; WAM S36742 (8 preserved specimens), WAM S36445 (6 shells) from 15°04'36"S, 125°11'18"E; AM C471812 (3 preserved specimens), WAM S37682 (6 preserved specimens) from 15°04'30"S, 125°11'21"E; WAM S37691 (2 preserved specimens)15°04'19"S, 125°11'18"E.

Etymology

For the name of the brightest star in the constellation Centaurus, Alpha Centauri, a bright star that was important in naval navigation, noun in apposition.

Description

Shell (Figs. 208C, 215A–D): Small (D= 10.8–14.3 mm; Table 11), delicate, discoidal to very broadly conical with low spire; periphery well rounded to slightly angulate, whorls separated by rather shallow suture; umbilicus narrowly open, ~ 1 mm wide, 30–90% concealed; yellowish brown. Last whorl very strongly descending behind aperture; angle of aperture 15–30°; elongate, simple, inside whitish, with moderately expanded, weakly reflected, thin lip; palatal node absent, basal node well developed. Protoconch 1.7 mm in diameter, comprising one whorl, with very fine, sparse pustules. Teleoconch smooth, with well-developed radial growth lines; microsculpture comprises sparsely distributed, fine periostracal setae, worn in adult shells giving them a

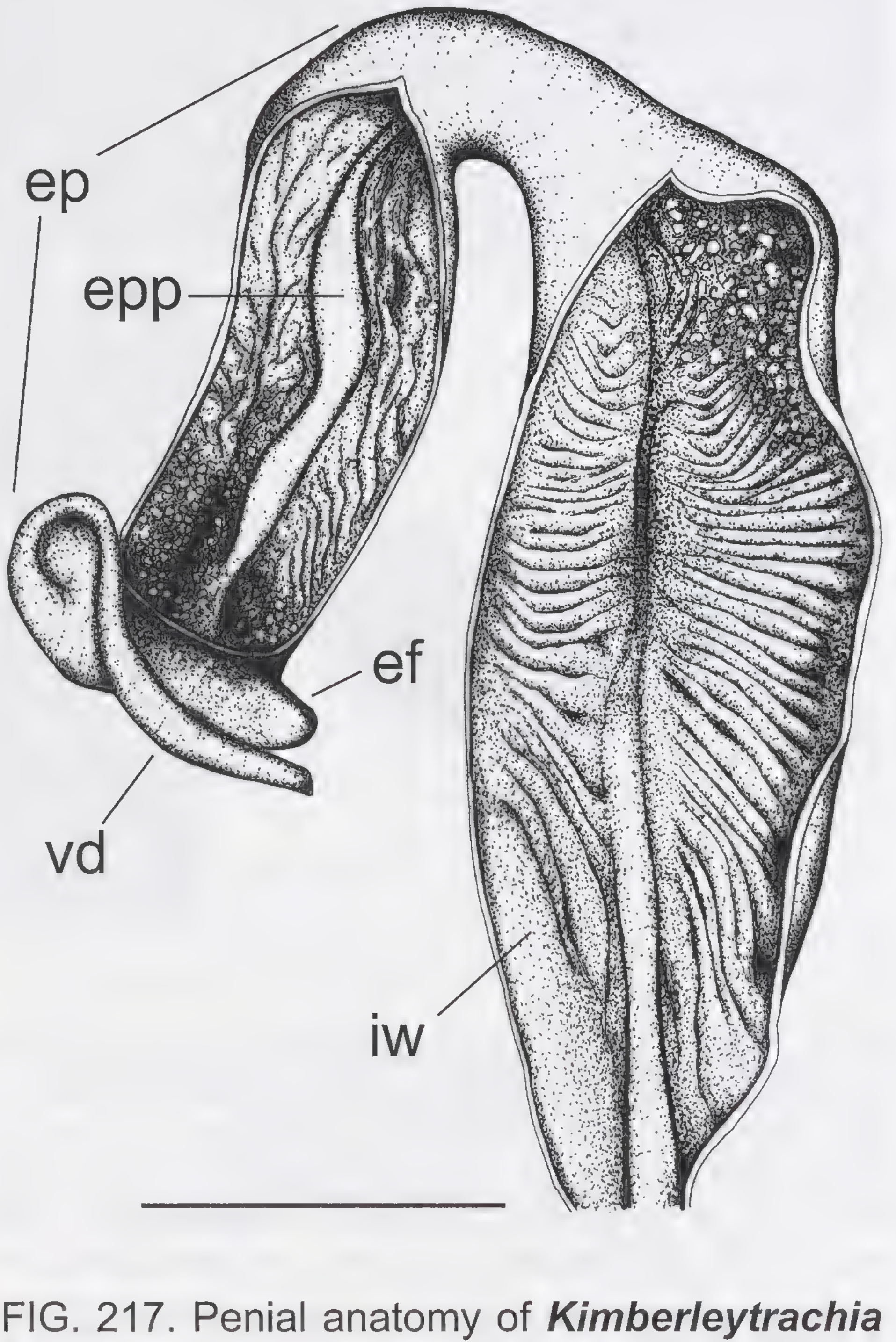

FIG. 217. Penial anatomy of ***Kimberleytrachia alphacentauri*** n. sp. paratype AM C471810 (Boongaree Island, August). Scale bar = 3 mm.

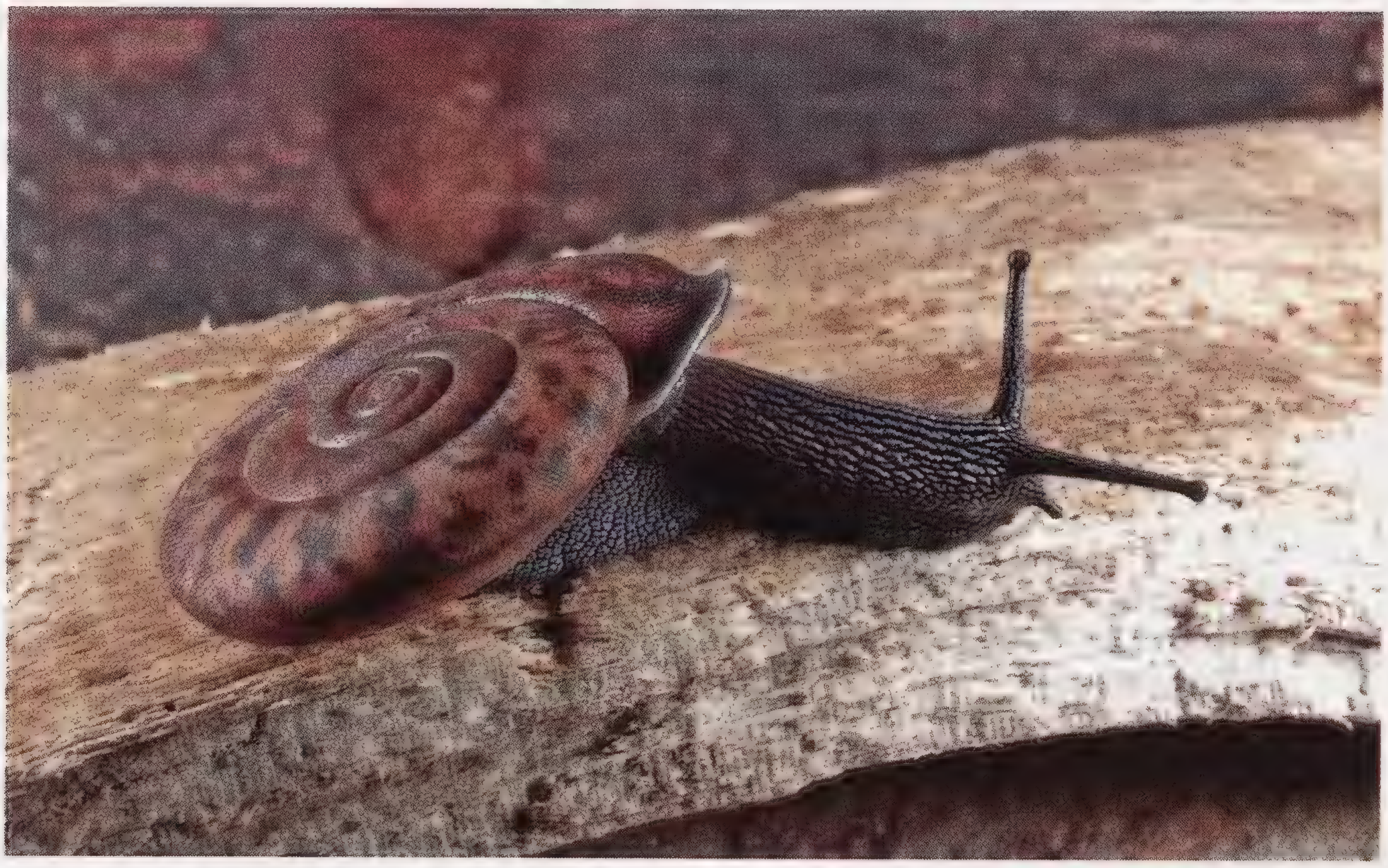

FIG. 218. Photograph of living holotype of ***Kimberleytrachia aequum*** n. sp.

glossy shine; inner umbilical whorls covered with some pustules.

Digestive anatomy (Fig. 215E–G): Jaw consisting of about 10 plates. Radula C + 12–14 + 3–4 + 20–22.

Genital anatomy (Figs. 216–217): Penis elongate, tubular, longer than vagina. Inner penial wall with regularly arranged, lateral lamellae which gradually become more oblique proximally; distal end of wall supporting some irregularly arranged, small pustules; a longitudinal gutter forms along entire length of inner penial wall separating lateral lamellae in the middle. Epiphallus bent, much shorter than penis; inner wall supports very fine, irregular pustulation near proximal end near opening to deferens, irregular longitudinal folds plus one strong longitudinal pilaster form along entire length; flagellum very short. Penial retractor muscle stubby. Vas deferens entering near distal end; thin. Vagina much longer than free oviduct.

Mitochondrial Differentiation

Infraspecific genetic distance (3 sequences): 0.001–0.006; interspecific genetic distances: 0.272–0.274 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.081–0.113 to all other congeners (13 sequences, 6 species).

Comparative Remarks

Shell significantly smaller than other species treated here. *Kimberleytrachia deflecta* from Prince Regent Reserve is similar with respect to shell shape, size and sculpture but differs most significantly in anatomy of inner penial wall (i.e., lack of regularly arranged, lateral lamellae). Armature of inner penial consisting mainly of lateral lamellae is characteristic (only similar in ***K. somniator***).

Distribution (Fig. 207)

Boongaree Island.

Kimberleytrachia aequum n. sp.

Figs. 218–220

Type Locality

Western Australia, northwestern Kimberley, Bonaparte Archipelago, Boongaree Island.

Material Examined

Holotype WAM S29303 (isolated soft body without shell; Fig. 218).

Etymology

From "*aequum*" (Latin = flat) for its flattened shell; noun in apposition.

Description

Shell (Fig. 218, living animal): Known only from a photograph, medium sized, with about

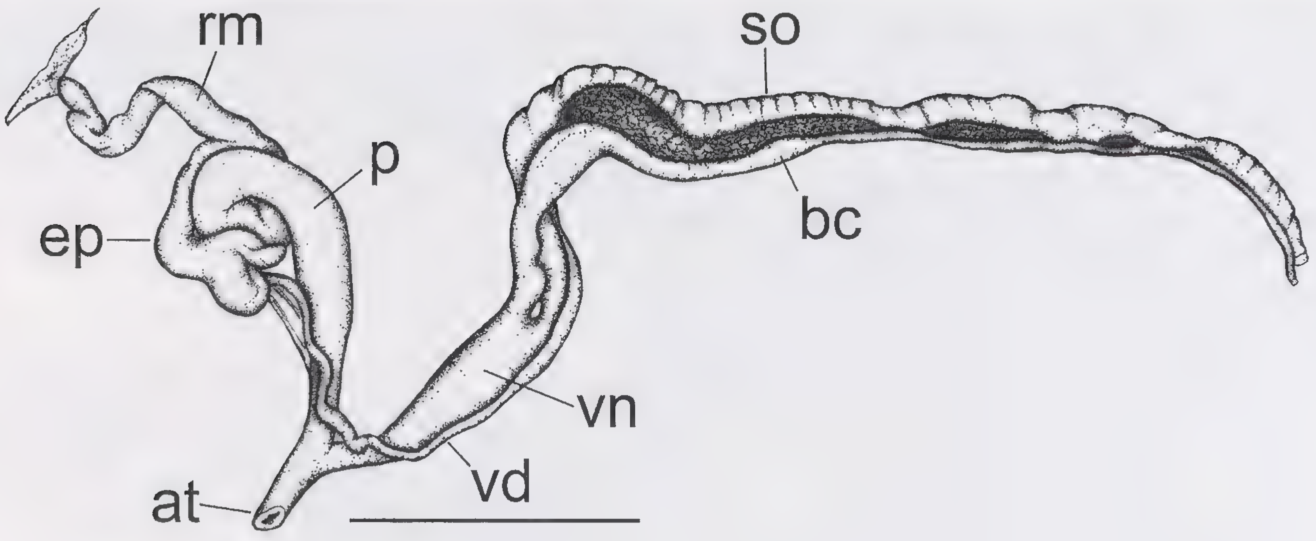

FIG. 219. Genital anatomy of ***Kimberleytrachia aequum*** n. sp. holotype WAM S29303 (Boongaree Island, February). Note that distal parts of spermoviduct, bursa copulatrix and albumen gland are lacking. Scale bar = 5 mm.

five whorls, almost perfectly dicoidal in shape with flat spire, thin and translucent, with well-rounded periphery; essentially smooth with well-developed microsculpture of dense periostracal setae that cover the entire shell; last whorl descending behind aperture; apertural lip well expanded.

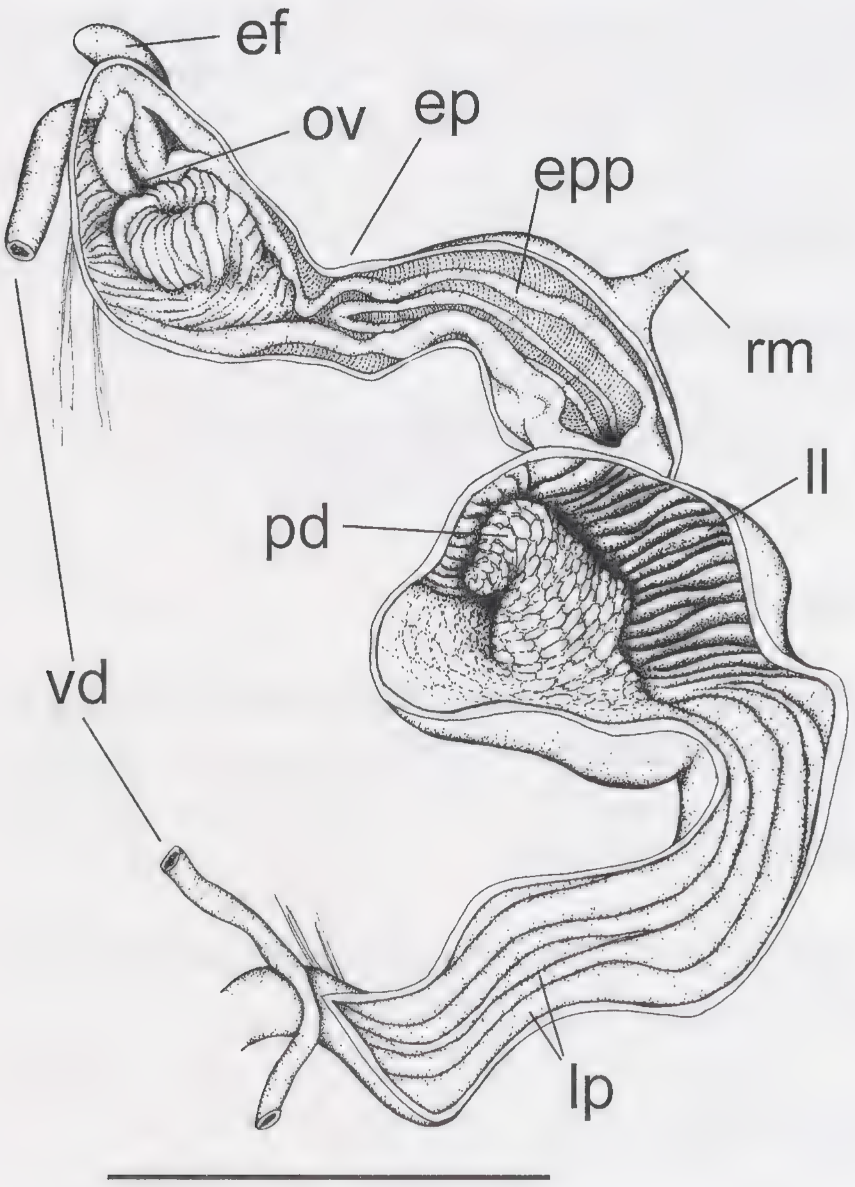

FIG. 220. Penial anatomy of ***Kimberleytrachia aequum*** n. sp. holotype WAM S29303 (Boongaree Island, February). Note that most distal part of spermoviduct, bursa copulatrix and albumen gland are lacking. Scale bar = 3 mm.

Genital anatomy (Figs. 219–220): Penis elongate, moderately long, about same length as vagina. Distal half of inner penial wall with well-developed lateral lamellae; proximal half supporting strong longitudinal pilasters; underneath opening to epiphallus densely packed and partly fused pustules form pad-like elevated structure. Epiphallus bent, slightly shorter than penis; inner wall with two strong and two thinner longitudinal pilasters; at distal end near opening to vas deferens and flagellum a collar is formed by elevated pilasters; flagellum short. Penial retractor muscle comparatively long. Vas deferens entering near distal end; thin. Vagina longer than free oviduct.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.226 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.095–0.125 to all other congeners (13 sequences, 6 species).

Comparative Remarks

The holotype is the only known specimen. It was photographed alive but the shell was subsequently eaten by other snails; remaining body parts permitted dissection of most parts genitalia as well as DNA sequencing. From information available, it is clear that ***K. aequum*** is distinct from any other known species on Boongaree Island as well as the mainland. It is characterised by an almost perfectly dicoidal shell and by a peculiar anatomy of the inner penial wall, which supports a complex armature of strongly developed longitudinal pilasters that are corrugated at their distal end. In addition,

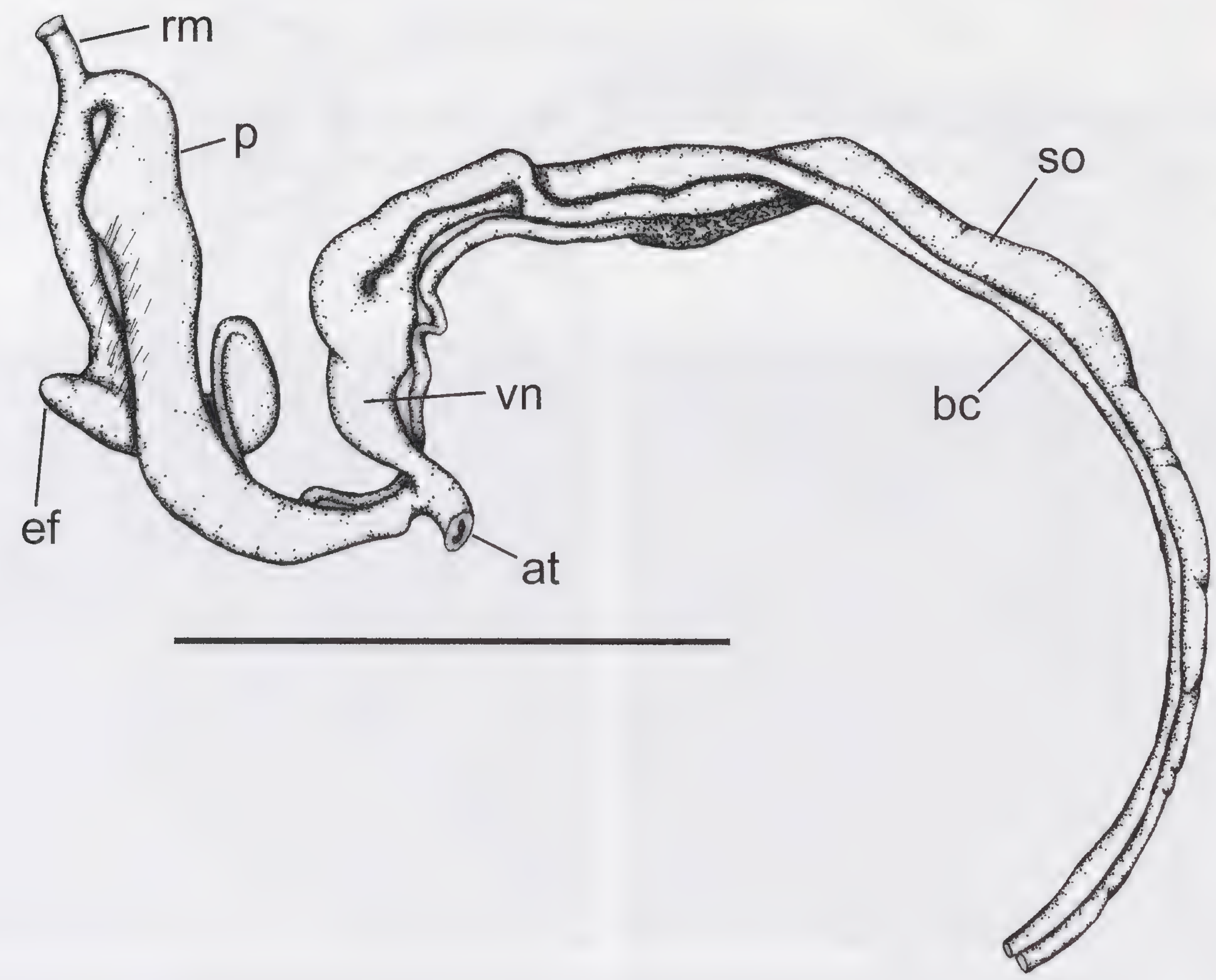

FIG. 221. Genital anatomy of ***Kimberleytrachia hirsuta*** n. sp. holotype WAM S37643 (1.3 km S of Halfway Bay, February). Note that distal parts of spermoviduct, bursa copulatrix and albumen gland are lacking. Scale bar = 5 mm.

complex armature of inner penial and epiphallic walls is characteristic. ***Kimberleytrachia canopi*** has a similarly complex penial wall armature, which comprises corrugated lamellae, but a more complex armature of the epiphallic wall.

Distribution (Fig. 207)

Boongaree Island.

Kimberleytrachia hirsuta n. sp.

Figs. 221, 222

Type Locality

Western Australia, central Kimberley coast, Hanover Bay, Munster Water, mainland 1.3 km S of Halfway Bay of, 15°20'15"S, 124°49'23"E; coll. Vince Kessner, 11/02/2009, KIS 3–133 (S-facing vine thicket at the base of sandstone cliffs; in crevices).

Material Examined

Holotype WAM S37643 (preserved specimen).

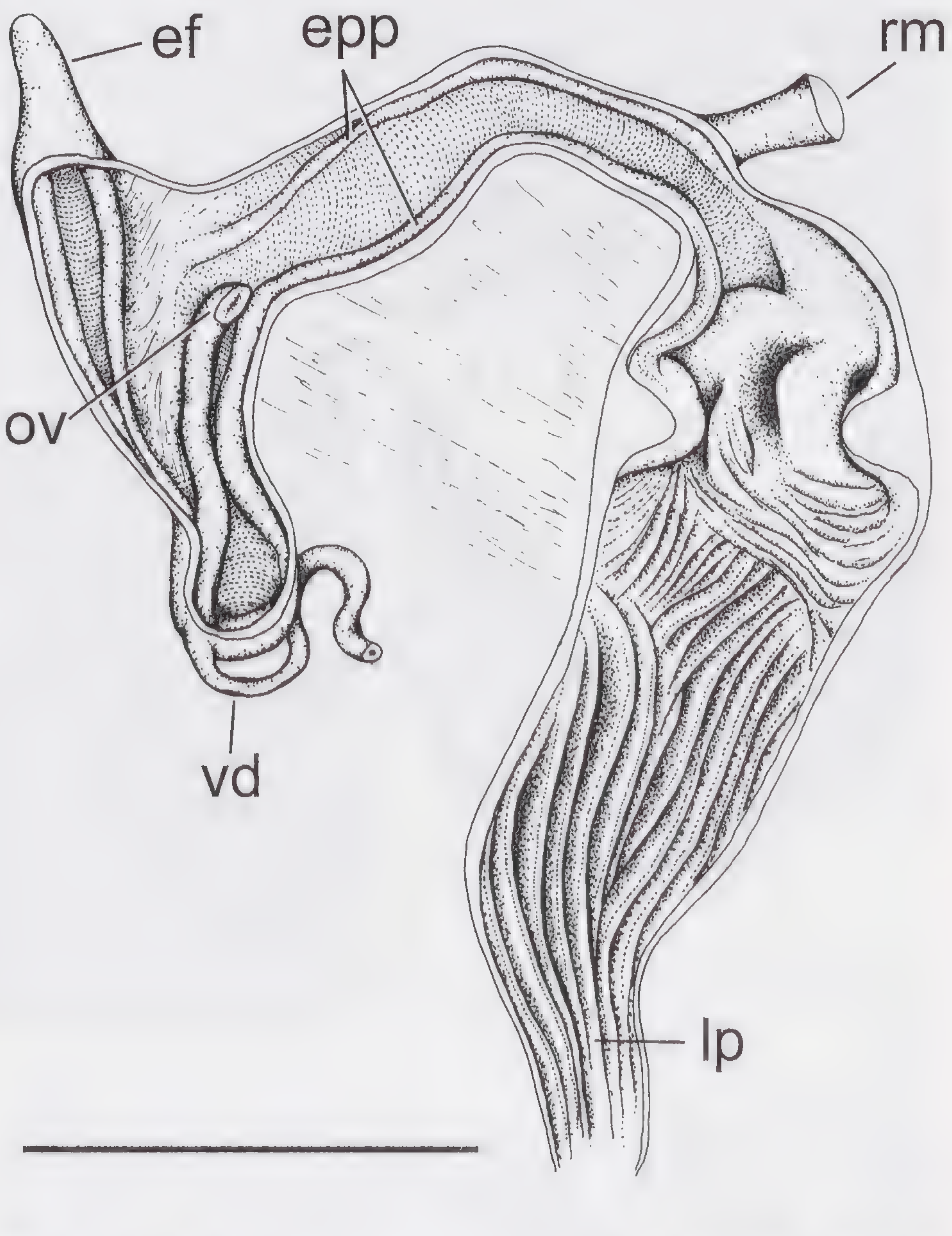

FIG. 222. Penial anatomy of ***Kimberleytrachia hirsuta*** n. sp. holotype WAM S37643 (1.3 km S of Halfway Bay, February). Scale bar = 2 mm.

Etymology

From "*hirsute*" (Latin = hairy), for the well-developed sculpture of periostracal setae on the shell of the holotype; adjective of feminine gender.

Description

Shell: Moderate to large in size (D = 18.6 mm, mature specimen), delicate to thin, very broadly conical with low spire; periphery well

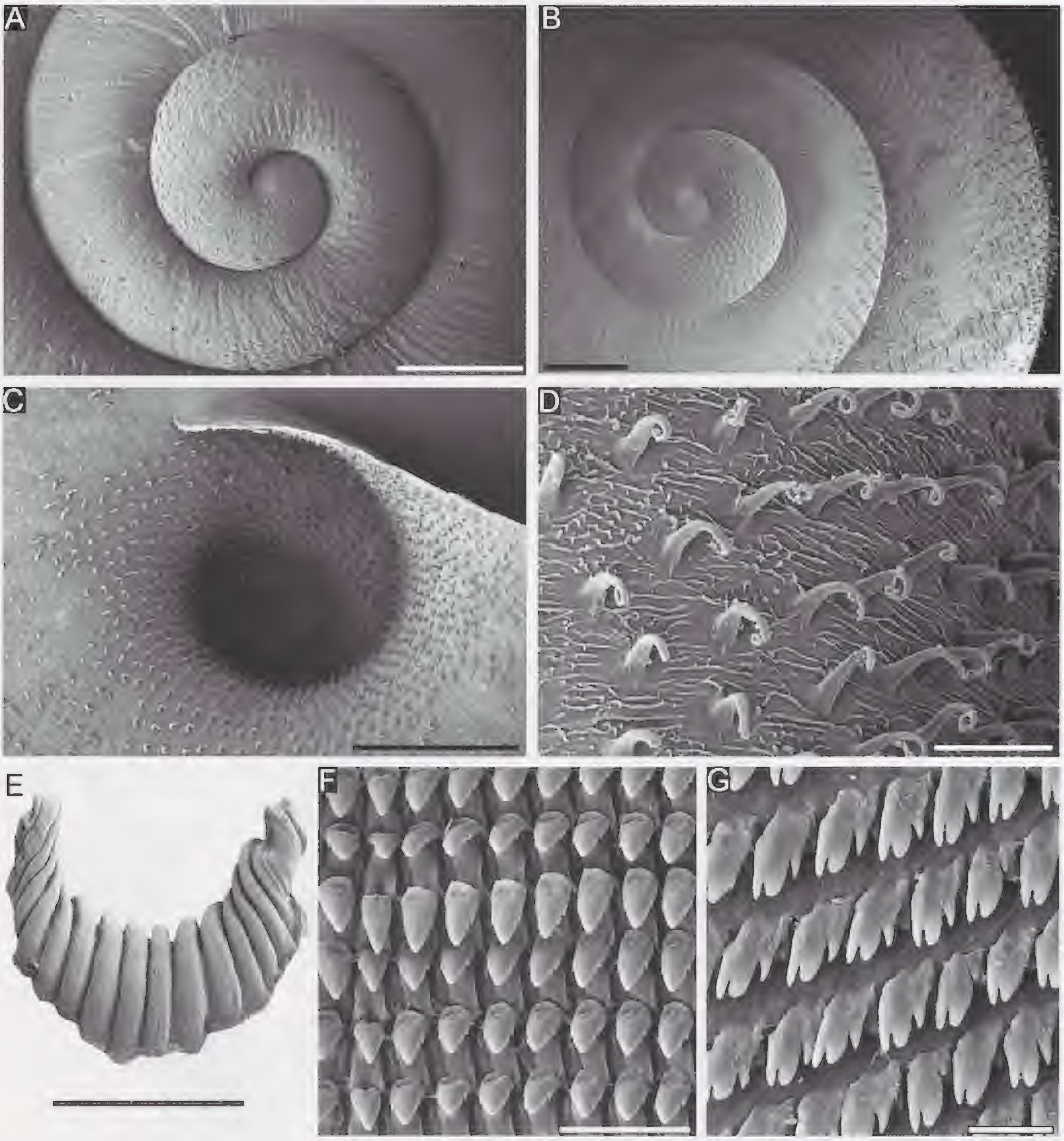

FIG. 223. SEM micrographs of ***Kimberleytrachia chartacea*** n. sp. (Uwins Island). A–D: Shell. A: Apical view showing protoconch, paratype WAM S37353; B: Sculpture across first whorls of shell viewed from above; C: Umbilicus; D: Close-up of micro-sculpture on last whorl. B–D: paratype WAM S37355 (juvenile shell). Scale bars A–C = 1 mm, D = 100 µm; E: Jaw paratype AM C471813. Scale bar = 500 µm; F–G: Radula paratype AM C471813. F: Central and inner lateral teeth viewed from above. Scale bar = 50 µm; G: Middle marginal teeth viewed from above. Scale bar = 20 µm.

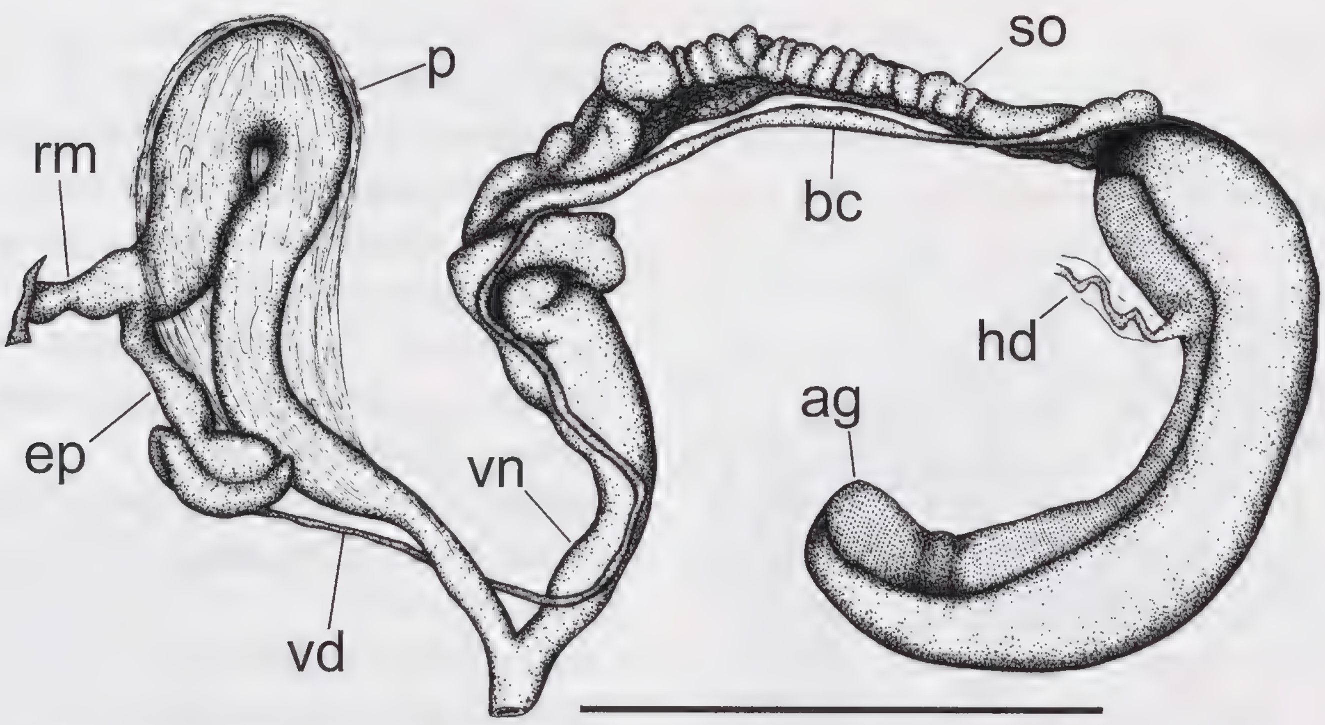

FIG. 224. Genital anatomy of ***Kimberleytrachia chartacea*** n. sp. paratype AM C471813 (Uwins Island, June). Scale bar = 10 mm.

rounded, whorls separated by rather shallow suture; umbilicus ~ 3 mm wide, not concealed; yellowish brown. Aperture elongate, simple. Teleoconch smooth, with faint radial growth lines, densely covered with fine periostracal setae, regularly arranged in radial pattern; inner umbilical whorls with well-developed pustules that support long setae.

Genital anatomy (Figs. 221–222): Penis elongate, longer than vagina. Distal end of inner penial wall supporting dense lateral lamellae; proximal two thirds supporting narrow, well-developed longitudinal pilasters; pad-like thickening forms underneath opening to epiphallus. Epiphallus bent, shorter than penis; inner wall essentially smooth, one longitudinal pilaster forming along entire length, two additional pilasters form at distal end, reaching into short flagellum. Penial retractor muscle short. Vas deferens entering near distal end, extending into lumen of epiphallus; thin. Vagina about same length as free oviduct.

Comparative Remarks

The holotype is a subadult specimen with unfinished apertural lip and was not photographed. Shell differs from other congeners by very pronounced development of periostracal setae being visible with naked eye. Distinctive features of genital anatomy are well-developed, narrowly arranged lateral lamellae of inner penial wall and essentially smooth epiphallic wall.

Distribution (Fig. 207)

Mainland near Halfway Bay, west of Prince Regent Reserve.

Kimberleytrachia chartacea n. sp.

Figs. 208D, 223–225

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Hanover Bay, Uwins Island, 15°15’32”S, 124°48’08”E; coll. Vince Kessner, 9/06/2008, KIS 3–106 (vine thicket and large fig trees on upper slopes, piles of sandstone rocks; in crevices, under overhangs).

Material Examined

Holotype WAM S58466 (preserved specimen, Fig. 208D). Paratypes AM C471813 (8 preserved specimens), WAM S37071 (18 preserved specimens), WAM S37358 (3 shells) from type locality; WAM S37064 (10 preserved specimens), WAM S37351 (shell) from 15°15’09”S, 124°48’10”E; AM C471814 (8 preserved specimens), WAM S37065 (10 preserved specimens) from 15°15’44”S, 124°48’08”E; AM C471815 (5 preserved specimens), WAM S37066 (11 preserved specimens), WAM S37352 (4 shells) from 15°15’52”S, 124°47’05”E; WAM S37067 (9 preserved specimens), WAM S37353 (2 shells) from 15°16’02”S, 124°48’09”E; WAM S37068 (8 preserved specimens), WAM S37354 (shell) from 15°15’25”S, 124°48’04”E; WAM S37069 (6 preserved specimens), WAM S37355 (3 shells) from 15°15’26”S, 124°48’08”E; WAM S37070 (7 preserved specimens), WAM S37356 (2 shells) from 15°15’36”S, 124°47’52”E; WAM S37357 (shell) from 15°15’45”S, 124°47’54”E.

Additional, non-type material. WAM S37642 (5 preserved specimens) from southern part

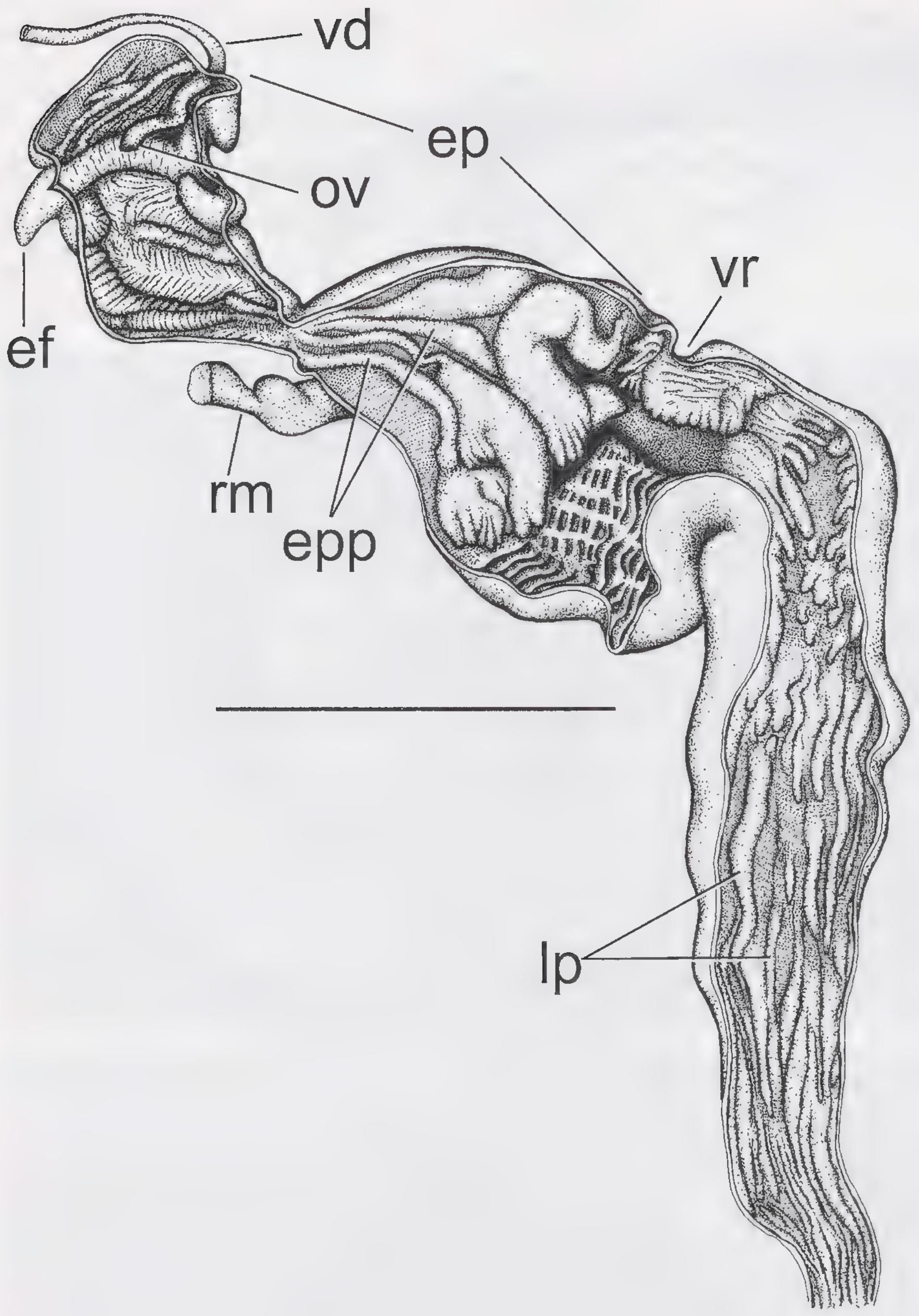

FIG. 225. Penial anatomy of ***Kimberleytrachia chartacea*** n. sp. paratype AM C471813 (Uwins Island, June). Scale bar = 5 mm.

of Uwins Island, 15°17'40.2"S, 124°47'58.4"E; WAM 37696 (preserved specimen), WAM S49039 (3 shells) from Mictyis Island, 2.5 km NW of Uwins Island, 15°13'12"S, 124°47'23"E.

Etymology

From "*chartaceus*" (Latin, masc = made from paper), for the delicate, transparent shell; adjective of feminine gender.

Description

Shell (Figs. 208D, 223A–D): Moderate to large in size (D = 18.8–22 mm; Table 11), very delicate, almost discoidal to very broadly conical with low spire; periphery well rounded to slightly angulated, whorls separated by well-incised suture; umbilicus ~ 3 mm wide, 10–30% concealed; colour yellowish brown to amber, with lighter base. Protoconch ~ 2.75 mm in diameter, comprising 1.5–2 whorls, with coarse pustules. Teleoconch essentially smooth; microsculpture of curled periostracal setae and fine ridglets, mostly worn in adult shells giving them a glossy shine; inner umbilical whorls with well-developed pustules that support setae. Last whorl strongly descending behind aperture. Angle of aperture 15–30°; wide, simple, inside with whitish suffusion, moderately to strongly expanded, weakly reflected, sharp lip; palatal node absent, basal node well developed.

Digestive anatomy (Fig. 223E–G): Jaw with more than 20 plates. Radula C + 17–19 + 3–4 + 22–23.

Genital anatomy (Figs. 224–225): Penis elongate, longer than vagina. Inner penial wall supporting densely arranged pilasters, partly fused, which gradually change orientation from lateral at distal to longitudinal at proximal end of inner penial wall; longitudinal gutter forms in centre of entire length of wall; pad-like thickening forms proximal of vergic ring. Epiphallus bent, shorter than penis; inner wall with complex armature consisting of longitudinal pilasters at proximal end and lateral lamellae at distal end; flagellum short. Penial retractor muscle short. Vas deferens entering near distal end; thin. Vagina about same length as free oviduct. Bursa copulatrix with inflated head.

Mitochondrial Differentiation

Infraspecific genetic distance (5 sequences): 0.0–0.010; interspecific genetic distances: 0.270–0.273 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.081–0.101 to all other congeners (10 sequences, 6 species).

Comparative Remarks

Similar to *K. deflecta* with respect to shell shape and lip development, but much larger in size. Shell flatter than that of ***K. somniator***, as indicated by a lower H/D ratio. Complex anatomy of inner penial wall highly characteristic.

Distribution (Fig. 207)

Uwins and Mictyis islands, Hanover Bay.

Kimberleytrachia amplirhagadoides n. sp.

Figs. 208E, 226–228

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, NW section of Augustus Island, 15°20'11"S, 124°31'10"E; coll. Vince Kessner, 13/02/2009, KIS 1–67 (vine thicket in valley on moderately steep W-facing slopes at base of sandstone cliffs; active on ground and boulders at night after rain).

Material Examined

Holotype WAM S58467 (preserved specimen, Fig. 208E). Paratypes WAM S37639 (2 preserved specimens), AM C471816 (3 shells), WAM 49018 (4 shells) from type locality; WAM S37075 (preserved specimen) from 15°19'58"S, 124°31'01"E; WAM S37346 (2 shells) from 15°21'05"S, 124°31'47"E; WAM S37347 (3 shells) from 15°20'59"S, 124°31'30"E; WAM S37348 (3 shells) from 15°21'24"S, 124°31'39"E; WAM S37072 (2 preserved specimens), WAM S37349 (2 shells) from 15°20'16"S, 124°31'16"E.

Etymology

Derived from the genus name *Amplirhagada* and the Greek suffix "-oides" (οειδες, an adjective suffix for nouns = like, resemble), for shell resembling that of some *Amplirhagada* species; noun in apposition.

Description

Shell (Figs. 208E, 226): Moderate to large in size (D = 20–22 mm; Table 11), delicate to thin, broadly conical with moderately elevated spire; periphery well rounded to slightly angulated, upper sector of whorls may be slightly shouldered, whorls separated by well-incised suture; umbilicus ~ 2 mm wide, 60–90% concealed; colour yellowish brown to amber, with lighter base. Protoconch ~ 2.5 mm in diameter, comprising one whorl, with coarse pustules. Teleoconch with faint radial growth lines, microsculpture of curled

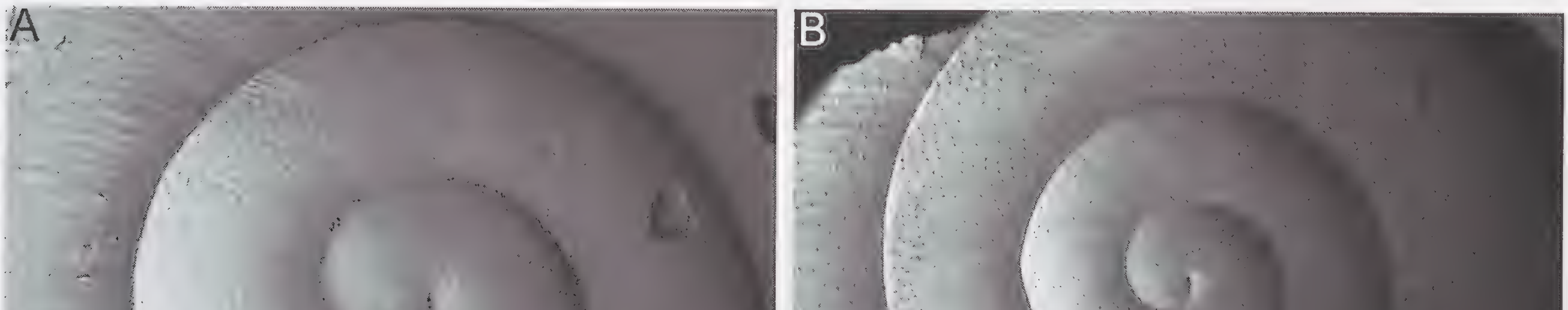

FIG. 226. SEM micrographs of the shell of ***Kimberleytrachia amplirhagadoides*** n. sp. (NW Augustus Island). A: Apical view showing protoconch and first whorl, paratype WAM S37348; B–C: Sculpture across first whorls viewed from above, paratype WAM S37346 (sub-adult shell). Scale bars = 1 mm; D: Close-up of micro-sculpture on last whorl, paratype WAM S37349. Scale bar = 100 μm.

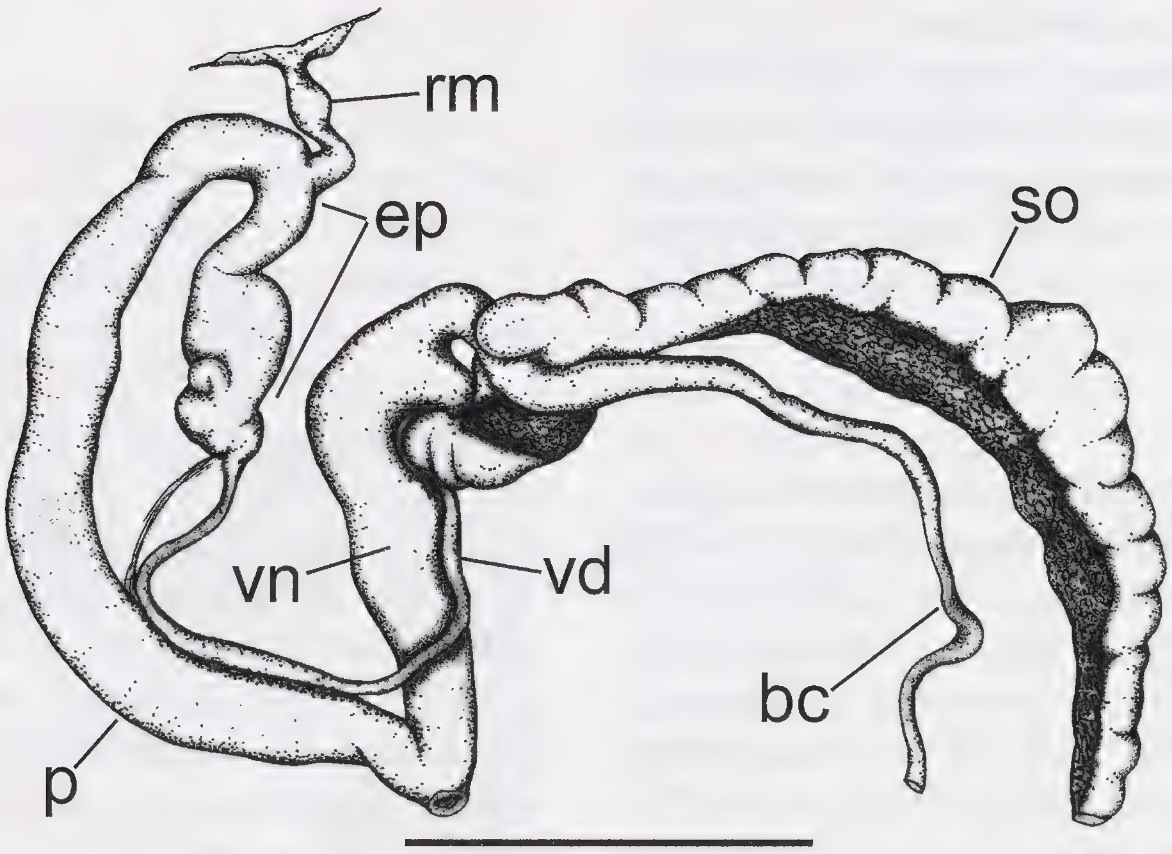

FIG. 227. Genital anatomy of ***Kimberleytrachia amplirhagadoides*** n. sp. paratype WAM S37639 (NW Augustus Island, February). Note that distal parts of bursa copulatrix and spermoviduct and albumen gland are lacking. Scale bar = 10 mm.

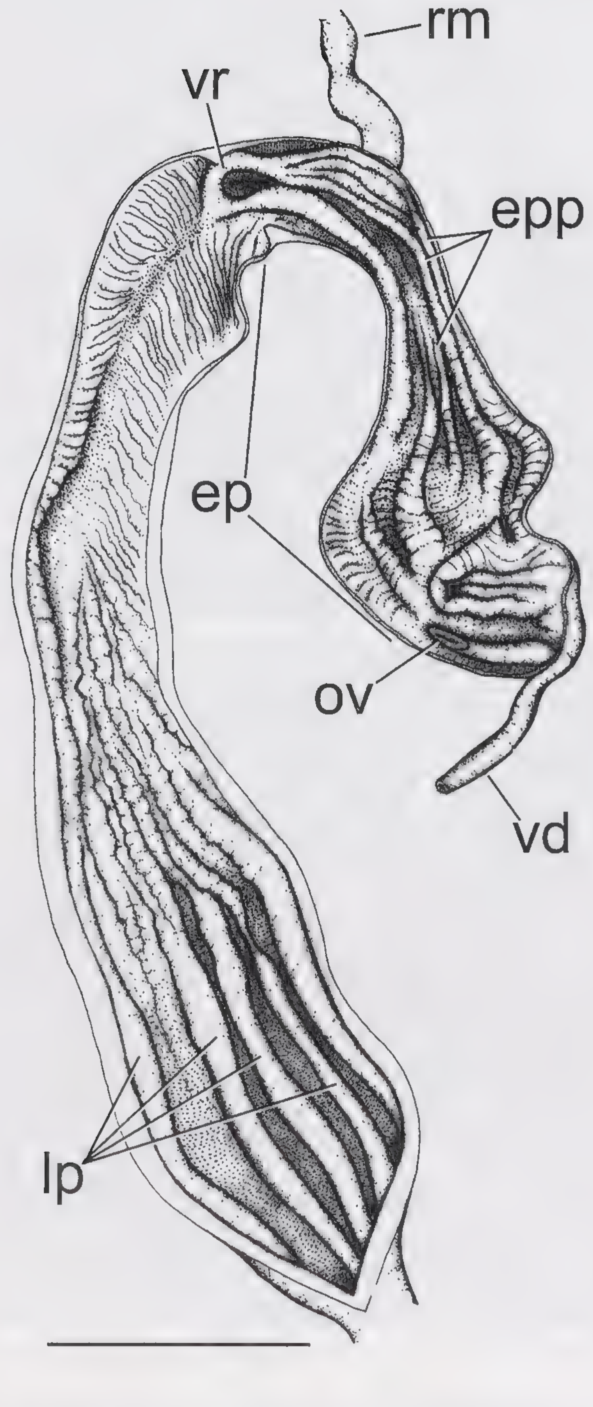

FIG. 228. Penial anatomy of ***Kimberleytrachia amplirhagadoides*** n. sp. paratype WAM S37639 (NW Augustus Island, February). Scale bar = 5 mm.

periostracal setae and fine ridglets, mostly worn in adult shells giving them a glossy shine; inner umbilical whorls with well-developed pustules that support setae. Last whorl weakly to moderately descending behind aperture. Angle of aperture 30–45°; wide, simple, inside with whitish suffusion, moderately to strongly expanded, weakly reflected, sharp lip; palatal node absent, basal node weakly to well developed.

Genital anatomy (Figs. 227–228): Penis elongate, longer than vagina. Distal end of inner penial wall supporting dense lateral lamellae, which are gradually transforming into well-developed, partly corrugated longitudinal pilasters at the proximal end. Epiphallus bent, shorter than penis; inner wall supporting several longitudinal pilasters along entire length. Penial retractor muscle short. Vas deferens entering near distal end, extending into lumen of epiphallus; thin. Vagina about same length as free oviduct.

Mitochondrial Differentiation

Infraspecific genetic distance (2 sequences): 0.003; interspecific genetic distances: 0.278–0.280 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.091–0.125 to all other congeners (13 sequences, 6 species).

Comparative Remarks

Typical are compared to other congeneric species high spire and almost subglobose shape, almost entirely concealed umbilicus, weakly descending aperture of shell, which resembles some shells of *Amplirhagada*. However, colouration and microsculpture are typical for ***Kimberleytrachia***. The species differs from ***K. somniator*** by narrower umbilicus, from ***K. alphacentauri*** by much larger size, and from ***K. chartacea*** by higher elevation of shell and wider cross-section of whorls. Anatomy of inner penial wall consisting of lateral lamellae (distal) and longitudinal ribs (proximal) plus presence of strong longitudinal pilasters on epiphallic wall are characteristic features.

Distribution (Fig. 207)

Northwestern section of Augustus Island.

Kimberleytrachia achernaria n. sp.

Figs. 208F, 229–231

Type Locality

Western Australia, central Kimberley coast, Brecknock Harbour, gully in the SE corner of Augustus Island, 15°23’45”S, 124°37’47”E; coll. Vince Kessner, 12/02/2009, KIS 2–71 (vine thicket patch along creek line, steep rocky slopes, sandstone; active at night on ground after rain).

Material Examined

Holotype WAM S58468 (preserved specimen, Fig. 208F). Paratypes AM C471817 (3 preserved specimens), WAM S37640 (6 preserved specimens), AM C471818 (2 shells), WAM S49024 (5 shells) from type locality.

Etymology

For the name of the brightest star in the southern constellation Eridanus, Archenar; adjective of feminine gender.

Description

Shell (Figs. 208F, 229): Moderate to large in size (D = 20–22 mm; Table 11), delicate to thin, broadly conical with moderately to conspicuously elevated spire; periphery well rounded, whorls separated by rather shallow suture;

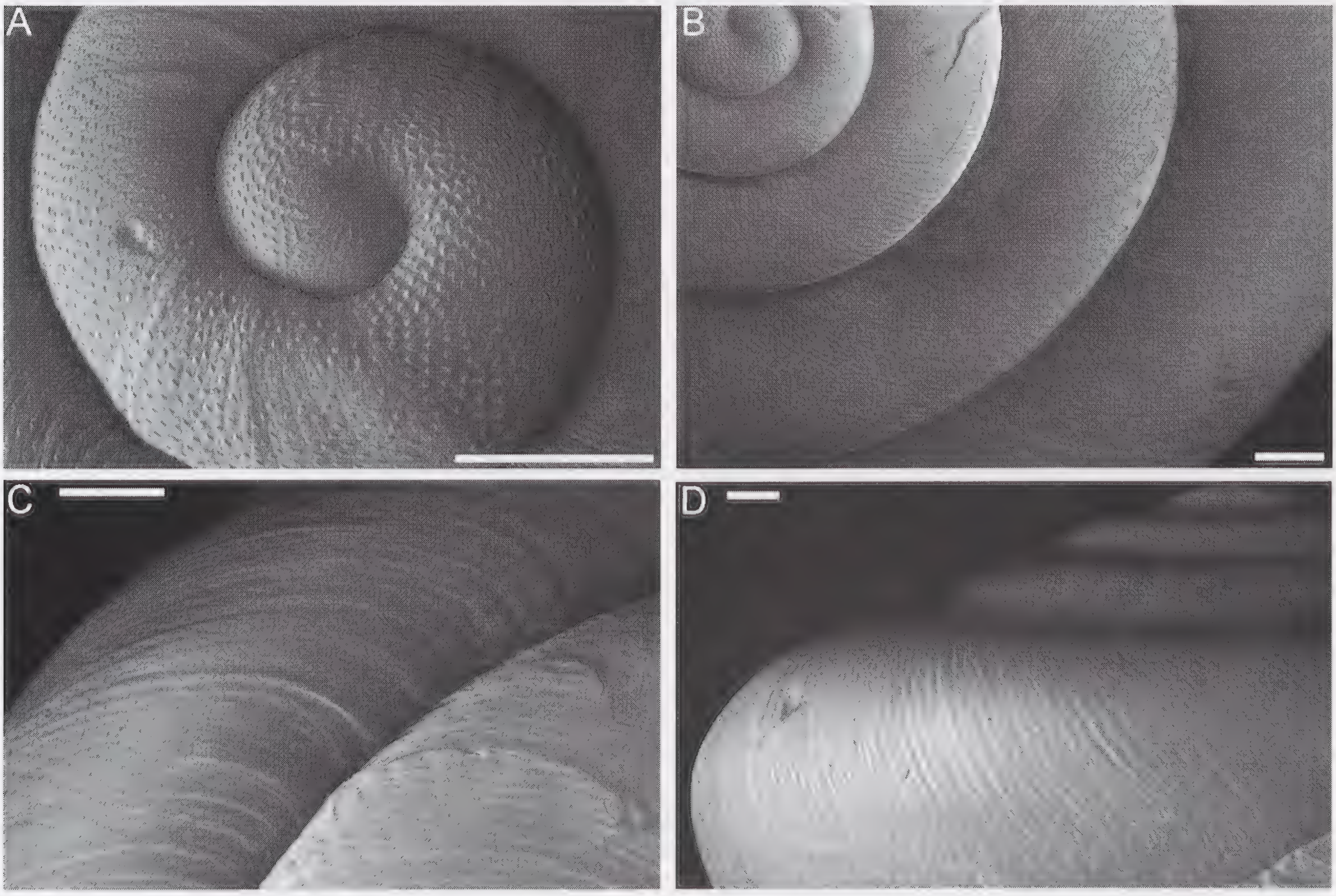

FIG. 229. SEM micrographs of the shell of ***Kimberleytrachia achernaria*** n. sp. paratype AM C471818 (SE Augustus Island). A: Apical view showing protoconch; B–C: Sculpture across first whorls viewed from above; D: Lateral view of shell. Scale bars = 1 mm.

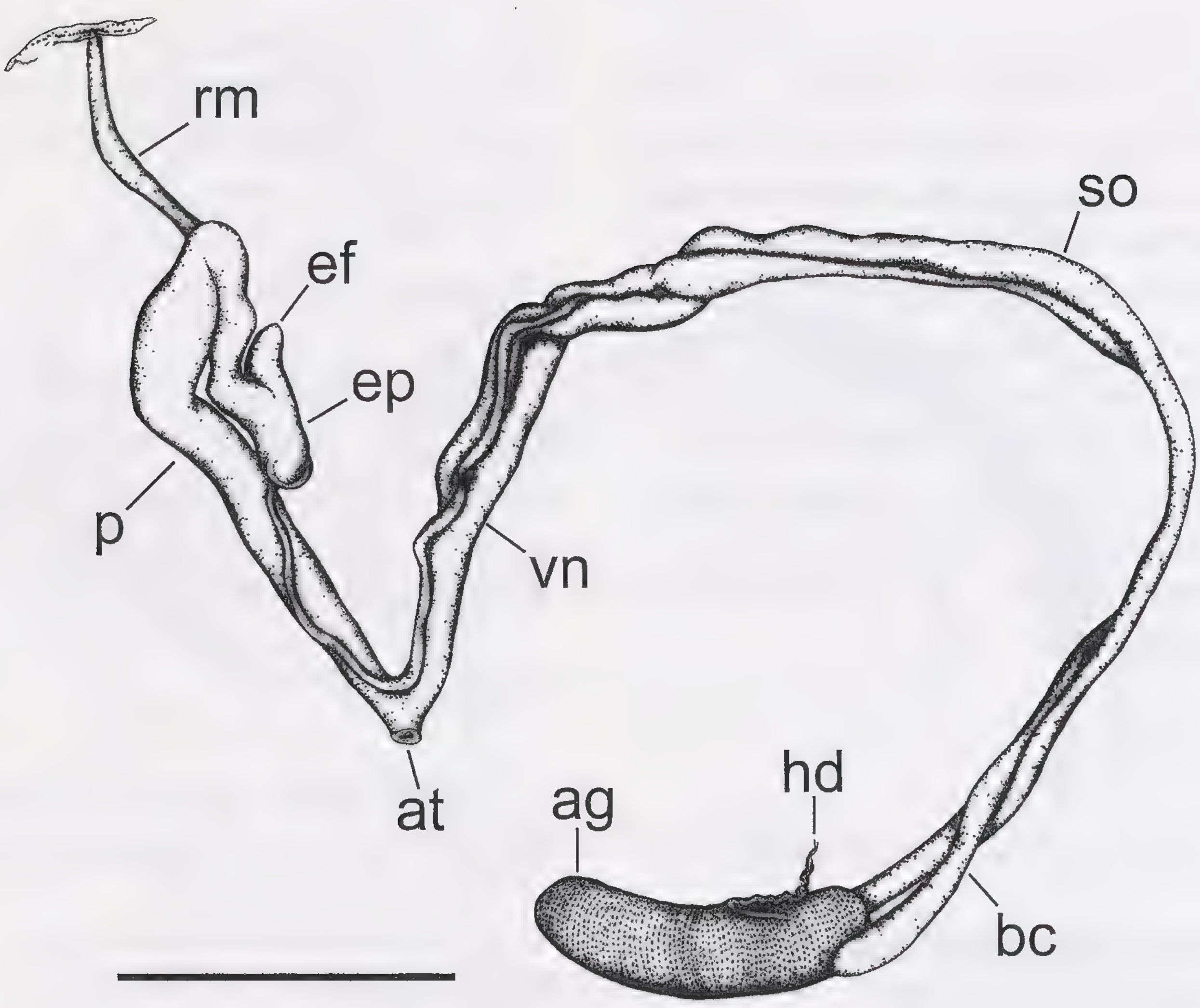

FIG. 230. Genital anatomy of ***Kimberleytrachia achernaria*** n. sp. holotype WAM S58468 (SE Augustus Island, February). Scale bar = 5 mm.

umbilicus ~ 2.5 mm wide, 10–30% concealed; colour yellowish brown, with whitish base. Protoconch ~ 2.5 mm in diameter comprising about one whorl, with coarse pustules. Teleoconch with faint radial growth lines, weakly developed microsculpture of very sparsely distributed periostracal setae, mostly worn in adult shells giving them a glossy shine; inner umbilical whorls with sparse pustules. Last whorl strongly descending behind aperture; angle of aperture ~ 30°; wide, simple, with moderately to strongly expanded, weakly reflected, sharp lip; palatal node absent, basal node weak to well developed.

Genital anatomy (Figs. 230–231): Penis elongate, longer than vagina. Distal end of inner penial wall supporting irregularly arranged lateral lamellae, proximal two thirds support narrow longitudinal pilasters, underneath opening to epiphallus a pad-like structure is formed, connected to longitudinal pilaster extending from epiphallic wall. Epiphallus bent, shorter than penis; inner wall supporting dense oblique lamellae plus one longitudinal pilasters along entire length, which extends into penial chamber connecting to pad; flagellum moderately long. Penial retractor muscle moderately long. Vas deferens entering near distal end, shortly extending into lumen of epiphallus; thin. Vagina about same length as free oviduct.

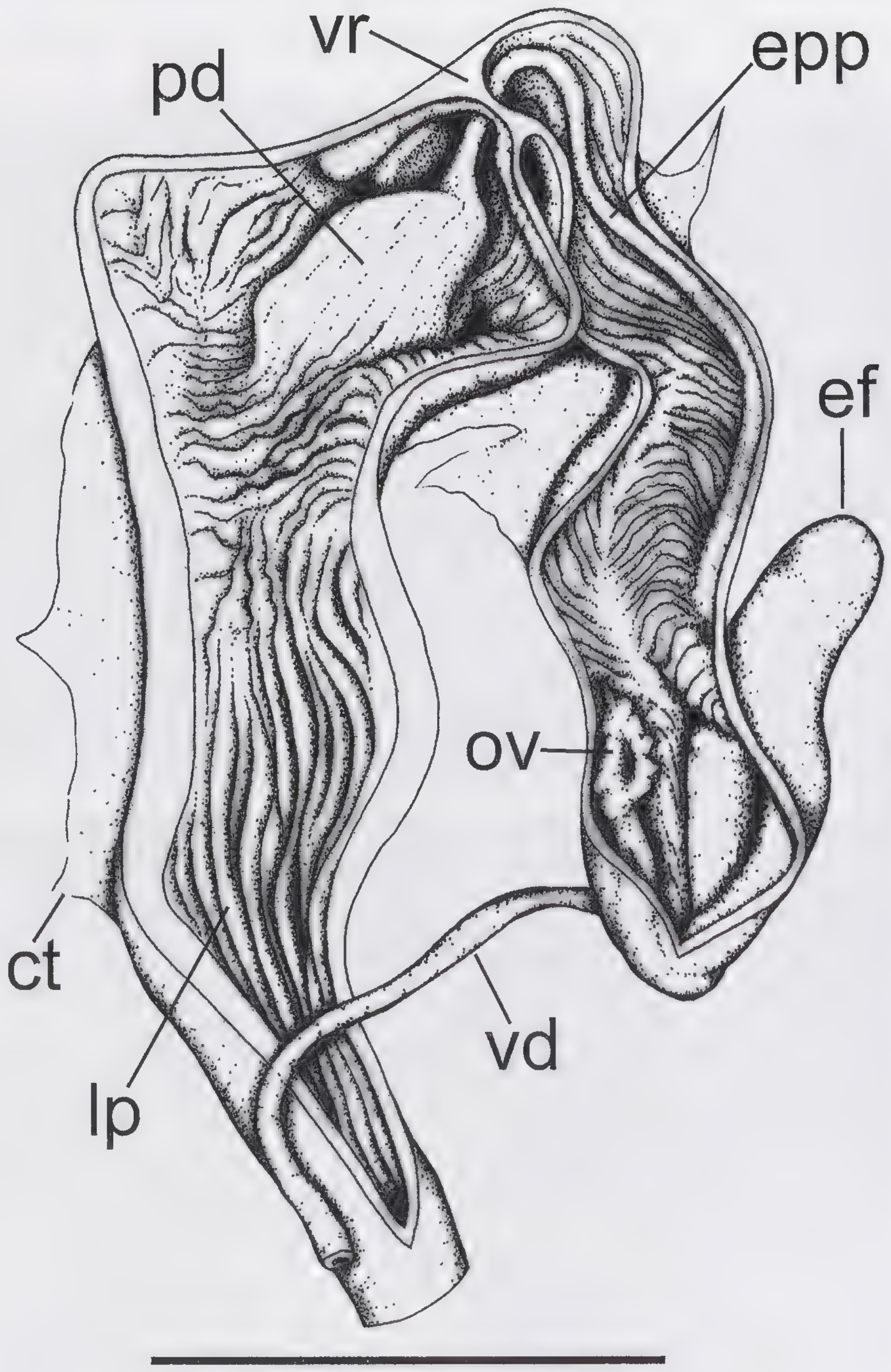

FIG. 231. Penial anatomy of ***Kimberleytrachia achernaria*** n. sp. holotype WAM S58468 (SE Augustus Island, February). Scale bar = 3 mm.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.283 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.082–0.103 to all other congeners (14 sequences, 6 species).

Comparative Remarks

Shell most similar to ***K. amplirhagadoides***, but comparatively flatter (wider diameter at same height); umbilicus not concealed, body whorl more strongly descending. Presence of large pad anterior to vergic ring being connected to a longitudinal pilaster extending from the epiphallus into penial lumen plus lateral lamellae at the epiphallic wall are typical features of this species.

Distribution (Fig. 207)

Southeastern section of Augustus Island.

Kimberleytrachia crucis n. sp.

Figs. 208G, 232–234

Type Locality

Western Australia, central Kimberley coast, Bonaparte Archipelago, Camden Sound, central section of D'Arcy Island, 15°17'25.3"S, 124°24'02.8"E; coll. Vince Kessner, 03/02/2009, KIS 1–62 (valley of seasonal stream, rock piles; active on ground at night after rain).

Material Examined

Holotype WAM S58469 (preserved specimen, Fig. 208G). Paratypes AM C471819 (preserved specimen), WAM S37641 (3 preserved specimens), AM C471820 (2 shells), WAM S37350 (4 shells), WAM S37073 (2 preserved specimens) from type locality.

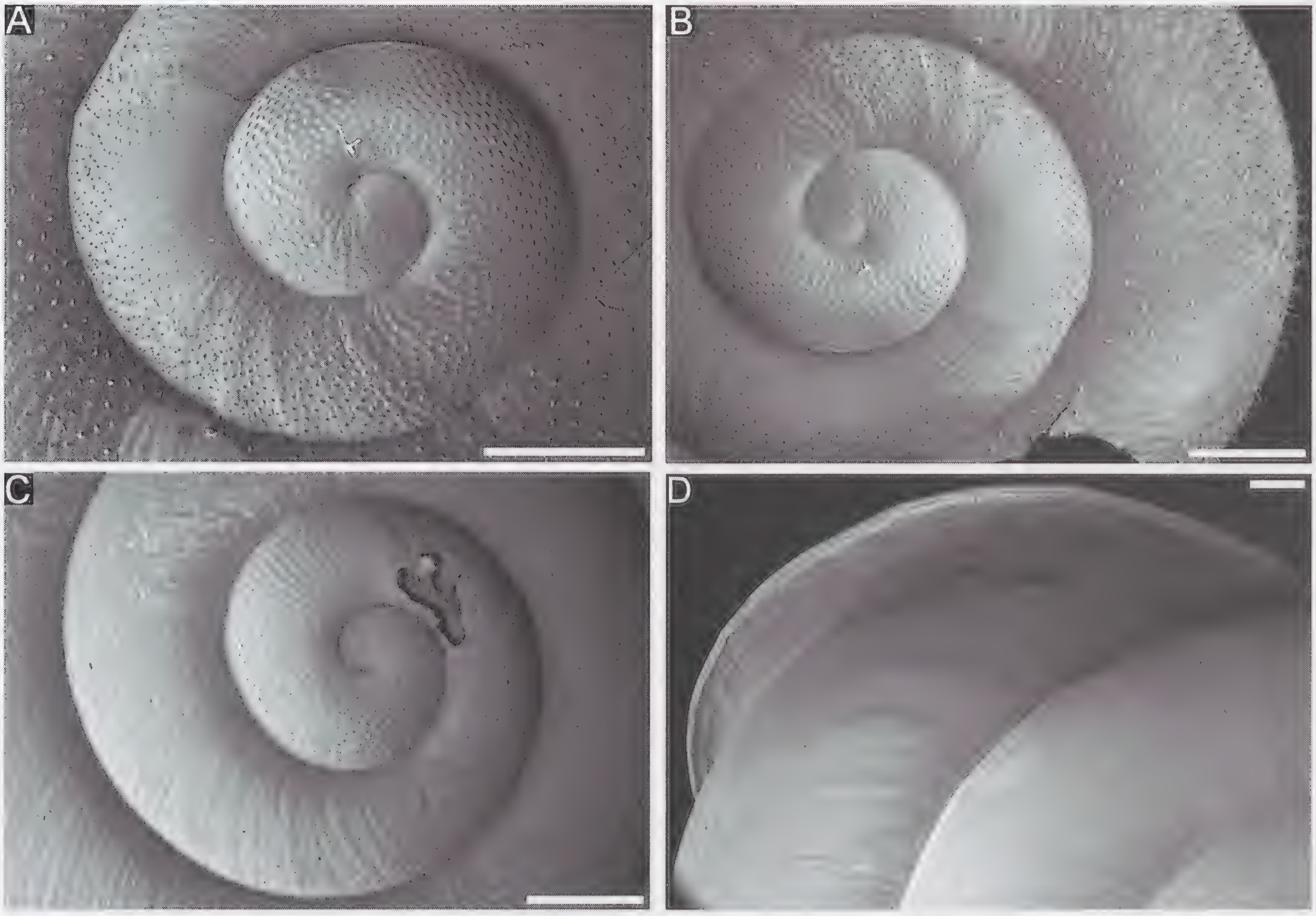

FIG. 232. SEM micrographs of the shell of ***Kimberleytrachia crucis*** n. sp. paratype AM C471820 (D'Arcy Island). A–B: Juvenile shell. A: Apical view showing protoconch; B: Sculpture across first whorls viewed from above; C–D: Adult shell. C: Apical view showing protoconch and first whorls; D: Close-up of last whorl near aperture viewed from above. Scale bars = 1 mm.

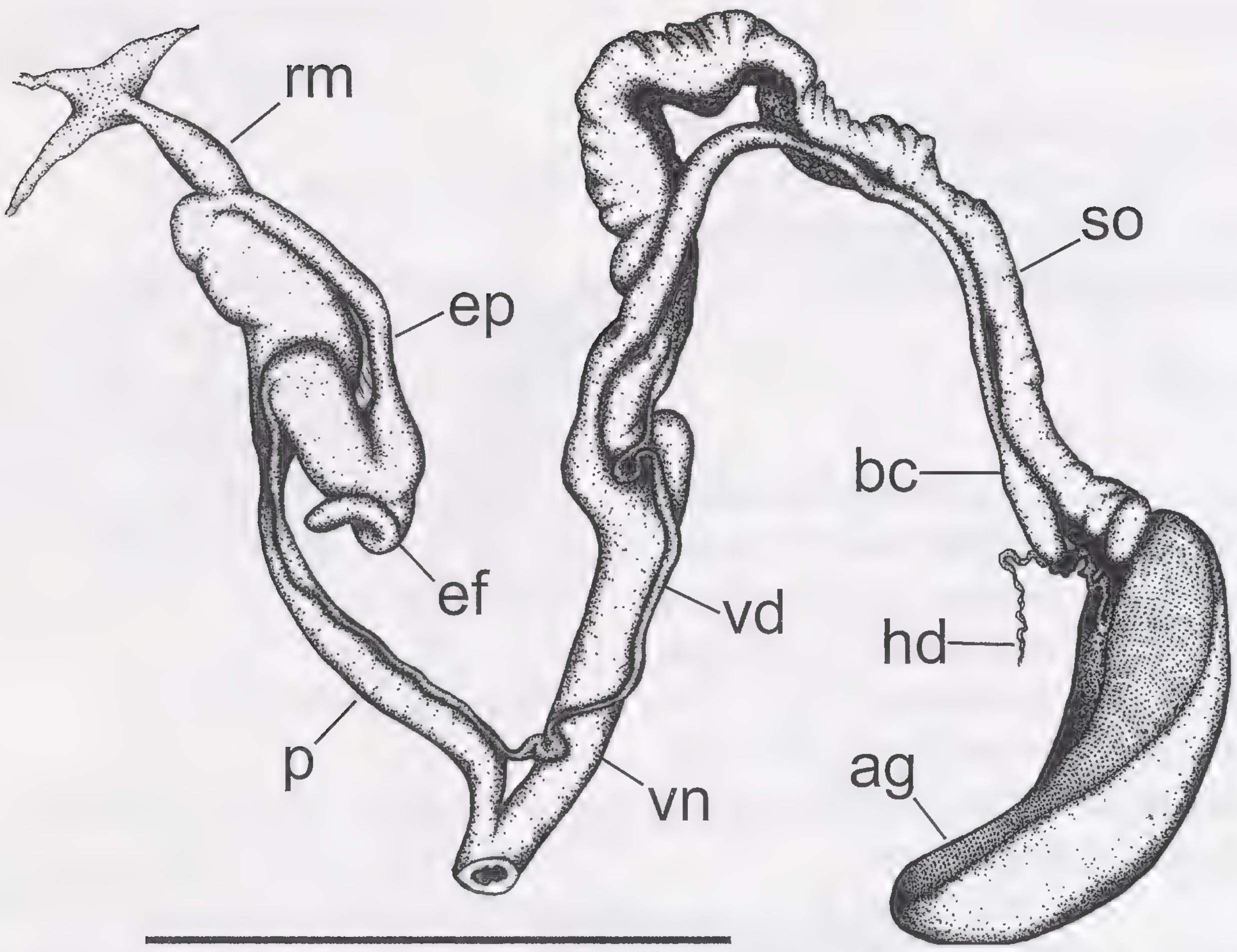

FIG. 233. Genital anatomy of ***Kimberleytrachia crucis*** n. sp. paratype WAM S37073 (D'Arcy Island, May). Scale bar = 10 mm.

Etymology

For the name of the constellation Southern Cross (Crux) of the southern sky; noun in genitive case.

Description

Shell (Figs. 208G, 232): Moderate to large in size (Table 11), delicate to thin, broadly conical with elevated spire; periphery well rounded, whorls separated by rather shallow suture; umbilicus ~ 2 mm wide, 30–70% concealed; colour yellowish brown, with whitish base; no banding. Protoconch ~ 2.5 mm in diameter, comprising about one whorl, with coarse pustules. Teleoconch with faint radial growth lines, microsculpture of periostracal setae, mostly worn in adult shells giving them a glossy shine; inner umbilical whorls with well-developed pustules that support setae. Last whorl weakly to moderately descending behind aperture; angle of aperture ~ 45°; wide, simple, with moderately to strongly expanded, weakly reflected, sharp lip; palatal node absent, basal node weak to well developed.

Genital anatomy (Figs. 233–234): Penis elongate, thin, about as long as vagina. Distal end of inner penial wall supporting dense lateral lamellae, proximal two thirds support narrow longitudinal pilasters, anterior to vergic ring a weak pad-like structure forms. Epiphallus bent,

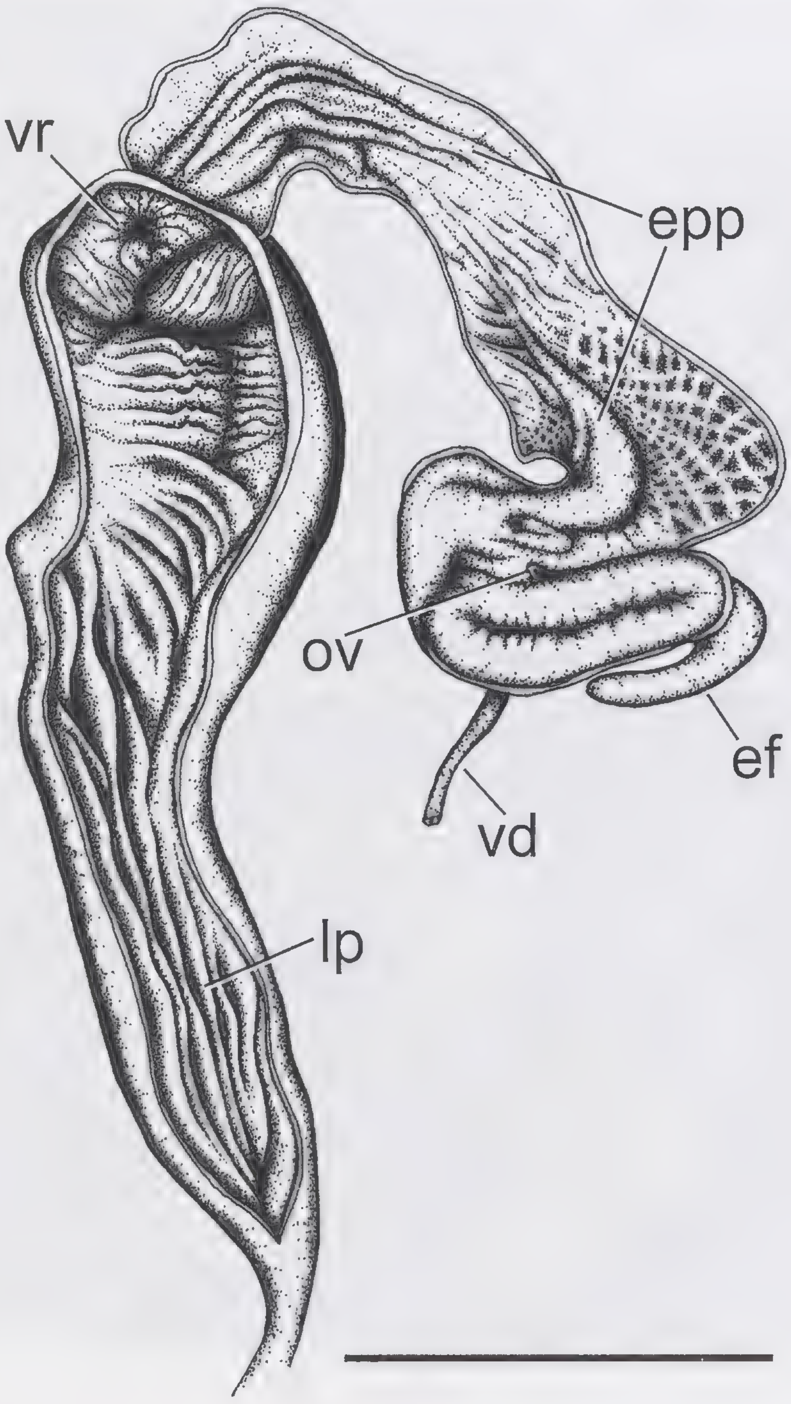

FIG. 234. Penial anatomy of ***Kimberleytrachia crucis*** n. sp. paratype WAM S37073 (D'Arcy Island, May). Scale bar = 3 mm.

shorter than penis; proximal end of inner wall supporting longitudinal pilasters, distal end supporting irregular net-like corrugations; flagellum short. Penial retractor muscle moderately long. Vas deferens entering near distal end, shortly extending into lumen of epiphallus; thin. Vagina longer than free oviduct.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.281 with respect to *K. crawfordi* from Storr Island (1 sequence), 0.092–0.120 to all other congeners (14 sequences, 6 species).

Comparative Remarks

Shell showing usual characters found in many other species except ***K. canopi*** and *K. deflecta*, which are much smaller, more elevated than that of *K. umbonis*, ***K. somniator***, and ***K. canopi***. Narrow longitudinal pilasters of inner penial wall similar only to ***K. achernaria*** and ***K. hirsuta***; from which it differs most conspicuously by complex armature of epiphallic wall (smooth in ***K. hirsuta***, with lateral lamellae in ***K. achernaria***).

Distribution (Fig. 207)

D'Arcy Island.

Kimberleytrachia crawfordi (Solem, 1979)
n. comb.
Fig. 208A

Torresitrachia crawfordi Solem, 1979: 91–92, pl. 7d–f; 1991: 182.

Type Locality

Western Australia, southwest Kimberley, Doubtful Bay, N of Walcott Inlet.

Taxonomic Remarks

This species was described based on one adult shell (plus a juvenile) from the type locality on the mainland while the anatomy has

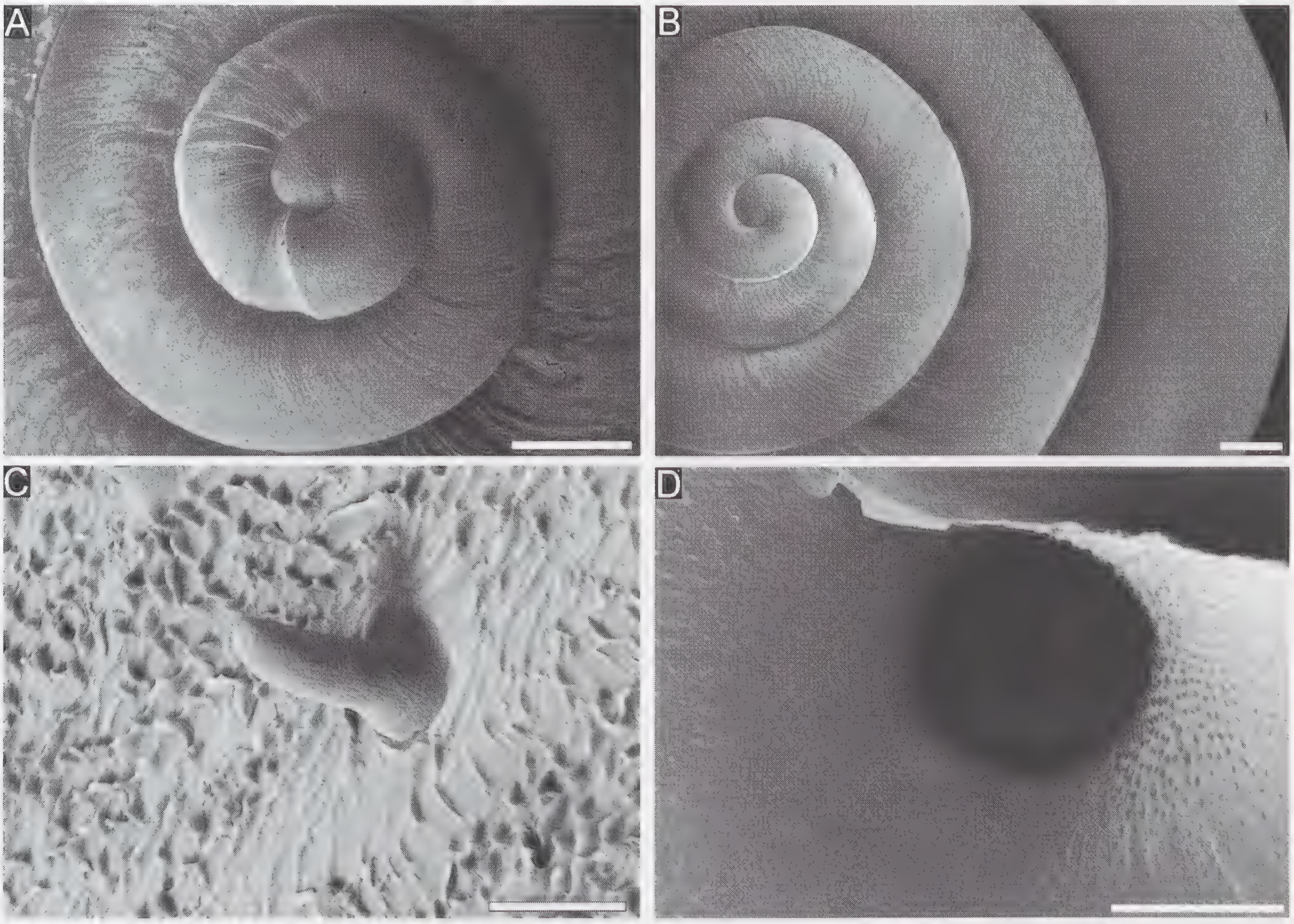

FIG. 235. SEM micrographs of the shell of *Kimberleytrachia crawfordi* AM C471821 (Storr Island). A: Apical view showing protoconch and first whorl; B: Sculpture across entire shell viewed from above; C: Close-up of periostracal hair; D: Umbilicus. Scale bars A–B, D = 1 mm, C = 50 µm.

remained unknown. Material from Storr Island is preliminarily subsumed under this name for the similar shell. Confirmation of the taxonomic status awaits comparative study of suitable material from Storr Island and the type locality on the mainland.

Material Examined

WAM S37790 (2 preserved juveniles), AM C471821 (2 shells), WAM S37833 (5 shells) from SE section of Storr Island, 15°56’54”S, 124°33’38”E; WAM S3782 (3 shells) from 15°56’39”S, 124°33’21”E.

Diagnosis

Shell (Figs. 208H, 235): Large (D = 21–23 mm; Table 11), delicate to thin, broadly conical with elevated spire; periphery well rounded, whorls separated by deep suture; umbilicus ~ 3 mm wide, 10–30% concealed; colour yellowish brown to amber, with lighter base. Protoconch 1.7 mm in diameter, comprising one whorl, with fine pustules. Teleoconch with faint radial growth lines, microsculpture of sparsely distributed periostracal setae and tiny ridglets, mostly worn in adult shells giving them a glossy shine; inner umbilical whorls with well-developed pustules. Last whorl weakly to moderately descending behind aperture. Angle of aperture 30–45° with the horizontal; wide, simple, with moderately to strongly expanded, weakly reflected, sharp lip; palatal node absent, basal node well developed.

Mitochondrial Differentiation

Interspecific genetic distances (1 sequence): 0.266–0.283 with respect to all other congeners (15 sequences, 7 species).

Comparative Remarks

Shell exhibits typical features known from other congeneric species except ***K. canopi*** and *K. deflecta*, which are much smaller; ***K. alphacentauri*** and ***K. amplirhagadoides*** differ by largely concealed umbilicus, ***K. hirsuta***, ***K. chartacea*** and ***K. somniator*** by denser shell pustulation. Juvenile status of material did not permit dissection of genital organs.

Distribution (Fig. 207)

Southwestern Doubtful Bay area, including Storr Island.

DISCUSSION

Systematic Significance of Morphological Characters

In his systematic revisions, Alan Solem has established the significance of characters of genital organs and shell for the classification of Western Australian camaenids (Solem, 1979, 1981a, b, 1985a, 1997). In general, the most informative and convenient source of systematic information are characters of genital anatomy, such as, in particular, presence/absence and development of penial features like epiphallus, flagellum, penial verge or penial sheath and penial wall sculpture (Table 12). The relative lengths and shapes of organs like penis, vagina and bursa copulatrix can also be diagnostic in some cases. If using genital characters for the identification of taxa, it is essential to bear in mind that the development and relative size of some features depend both on maturity of the animal and its actual reproductive state. Among fully mature specimens (with adult shell features and fully developed albumen gland), a simple pattern of seasonal variation is found with the genitalia being inactive and reduced in size during the early to middle dry season (~ May to August) (Solem & Christensen, 1984). Seasonal variation is observed with respect to the development of organs in general but also with respect to development of the sculpture of the penial or epiphallic walls. In aestivating animals, the inactive reproductive organs may be largely reduced in size and prominence (details of the inner wall sculpture). The descriptions given her take these phenomena into account in that differences in the development of features are not used to delimit taxa, in particular when it has been clear that genitalia were in a resting phase.

Solem (1981a) found in *Amplirhagada* that in sympatry species frequently differ conspicuously in the sculpture of their penial and vaginal walls. He suggested that these characters may play an important role in mate recognition and that this function drives the evolution of distinct penial characteristics in sympatric species. Recent findings of reproductive character displacement in the genital morphology of Asian camaenids (*Satsuma*) seem to provide evidence in support of this idea (Kameda et al., 2009).

In addition to genital characteristics, most genera are relatively easy to recognise by typical combination of shell features, which include overall size and shape, width and

TABLE 12. Comparative overview of genital characteristics of the camaenid genera of the Kimberley Islands (in alphabetical order).

Species	Penial sheath	Penial wall sculpture	Main stimulatory pilaster	Shape of vergic papilla	Epiphallus	Epiphallic flagellum	Epiphallic lobe	Bursa copulatrix
Amplirhagada	present	variable	absent/present	verge	absent/wanting	absent	absent	simple, short
Australocosmica	present	variable	absent	collar	absent	absent	absent	simple, short
Baudinella	absent	longitudinal pilasters	absent	ring	present	present	absent	S-folded, moderately long
Carinotrachia	present	complex pilasters	absent	pore	absent	absent	absent	simple, short
Globorhagada	present	smooth	absent	pore	absent	absent	absent	inflated, short
Kimberleydiscus	present	pustulation	present	simple	wanting	absent	absent	simple, short
Kimberleymelon	present	pustulation	present	simple	wanting	absent	absent	simple, short
Kimberleytrachia	absent	complex	absent	ring	present	present	absent	elongated
Kimboraga	present	pustulation	absent	ring or verge	absent	absent	absent	simple, short
Molema	absent	longitudinal pilasters	absent	verge	present	present	absent	kinked, moderately long
Retroterra	absent	complex pilasters	absent	verge	present	present	absent	kinked or coiled, moderately long
Rhagada	absent	smooth	absent	verge	present	present	absent	simple or kinked, moderately long
Setobaudinia	present	pustulation, transverse or longitudinal pilasters	absent	verge	present	present	present	elongated
Torresitrachia	absent	posterior pustules, anterior pilasters	absent	ring	present	present	absent	elongated
Xanthomelon	present	pustulation	absent	pore	absent	absent	absent	inflated

TABLE 13. Comparative overview of shell characteristics of the camaenid genera of the Kimberley Islands (in alphabetical order); *UW = Umbilical Width.

Species	H Range (mm)	D Range (mm)	Shape	Protoconch Sculpture	Teleoconch Sculpture	Periphery	Coloration	UW* relative to Shell	Covering of Umbilicus	Sealing when Aestivating
Amplirhagada	8–20	15–25	broadly subglobose to beehive	radial pustulation	fine growth lines to strong ribs, smooth base	rounded to angulated	banded or uniform	narrow	partly - entirely	free/rock
Australocosmica	9–17	13–18	subglobose	weak radial pustulation	strong ribs, smooth base	rounded	uniform, dark	narrow	partly - entirely	free
Baudinella	2.5–4.0	6.5–7.5	discoidal	crowded pustules	weak to strong axial ribs, microscopic setae or hairs	rounded	uniform, light	wide	not	free
Carinotrachia	9–12	15.5–18.5	broadly subglobose	strong radial pustulation	coarse radial ribs onto base, microscopic pustules	keeled	uniform, light	moderate	not	rock
Globorhagada	16–37	16–35	globose	faint radial growth lines	variable axial pustulation	depressed	uniform, light to dark	narrow	partly - entirely	free
Kimberleydiscus	8–11	18–22	discoidal	faint radial growth lines	fine growth lines only	sharply angulated	banded	moderate	not	?
Kimberleymelon	18–27	20–30	globose	faint radial growth lines	coarse growth lines	depressed	uniform, light	narrow	entirely	?
Kimberleytrachia	5–15	10–24	broadly subglobose	crowded radial pustules	microscopic setae, hairs, wavy ridglets	rounded	uniform, light	narrow	not - entirely	rock
Kimboraga	12–19	19–25	subglobose to globose	faint radial growth lines	faint growth lines to strong ribs onto base	rounded	uniform, dark	narrow	partly - entirely	rock
Molema	2.5–3.5	8–9	discoidal	crowded radial pustules	strong, noduled ribs onto base	rounded	uniform, dark	wide	not	free
Retroterra	5–13	13–24	discoidal	radial pustulation	growth lines to strong ribs into umbilicus	rounded	uniform, dark	wide	not	free
Rhagada	7–15	11–21	subglobose	faint axial riblets	axial riblets or ribs	rounded	banded	narrow	partly - entirely	free
Setobaudinia	3–11	6–21	discoidal	regularly arranged tubercles	microscopic setae or hairs	rounded	uniform, light	wide	not	free
Torresitrachia	6–11	12–20	discoidal to broadly subglobose	radial pustulation	axial ribs, microscopic setae or hairs, smooth base	rounded	uniform, light	narrow	not	free
Xanthomelon	18–26	20–30	globose	faintly pustulose	microscopic radial corrugations	depressed	uniform, light	narrow	partly - entirely	free

sealing of umbilicus as well as microsculpture of teleoconch and to a lesser degree the protoconch (Table 13). By contrast, it has been stated for eastern Australian camaenids that the microsculpture of the protoconch is an important taxonomic feature (Stanisic et al., 2010). However, with respect to the species level, Solem (1981a, b, 1997) found that shell features are prone to parallelism and that shells are often of limited value for delimitation and recognition of congeneric species. Shells often seem to reflect ecological adaptations to a certain type of habitat and life style. In *Amplirhagada* it has been found that allopatric species tend to exhibit similar shells whereas sympatric species often differ conspicuously in their shell morphology. It has been suggested that distinct shells in sympatry may reflect the adaptation to different ecological niches within the same habitat (Solem, 1981a). On a more general basis, this may also hold for species of different genera.

Contrary to shell and genitalia, features of the digestive anatomy were found to be widely conserved or homoplastic in camaenid land snails. This confirms observations of Solem (1981a, b, 1997), who stated that in Western Australian camaenids radula and jaws are of little value for taxonomic purposes. Similar observations were made in Asian (e.g., Chiba, 1999b; Kameda et al., 2007; Chiba & Davison, 2008) and New Guinean species (Jordaens et al., 2009).

Solem's (1981a) conclusions with regard to the significance of key morphological features for the delimitation and recognition of taxa have recently been confirmed for the most diverse genus, *Amplirhagada*, by a study that combined analyses of morphological and mitochondrial evidence (Köhler, 2010c). In this study it was shown that species as delimited by their anatomy were genetically well differentiated by on average 30% Tamura-Nei distances in the mitochondrial marker COI. Exceptionally, species were separated by as few as 10% sequence divergence only. However, even these amounts of genetic differentiation do not contradict a status as distinct species as suggested based on genital characters.

Patterns of Diversity and Distribution

In general, the distributional ranges of Kimberley camaenids are characterised by allopatry and micro-endemism. Solem (1991) stated that average species ranges are restricted to a diameter of 20 km on the Kimberley mainland. Our observations on the offshore islands are consistent with this finding. The surveyed islands vary in size from about 400 to 19,000 ha and all of them support endemic species. Exceptionally, few species occur on more than one island. Being inevitably restricted by island size, the average range of species is even smaller than on the mainland. However, island size is apparently not always a limiting factor. On the largest island, Augustus Island (~ 19,000 ha), all but one of the eleven species were found exclusively in either the northwestern or southeastern part. This observation suggests that here island size exceeds the range size of many species and that frequently species ranges are smaller than the 20 km diameter found by Solem (1991). This can be explained by two factors. Firstly, in the present revision a number of species as delimited by Alan Solem were found to be species complexes (e.g., *Globorhagada prudhoensis*, *Torresitrachia bathurstensis*, *Kimberleytrachia umbonis*). These examples may indicate that species were lumped together more frequently, which would have led to an overestimation of the size of species ranges. Secondly, observations in *Amplirhagada* suggest that there is a correlation between preferred habitat and the extent of ranges. In coastal areas, species are predominantly found in rainforest habitats but not in surrounding, more open wood- or bushland. Because rainforest vegetation is restricted to small pockets, these rainforest species are narrow range endemics found in one or few rainforest patches only (Solem, 1991; Köhler, 2010a). Further inland, however, where rainforest patches are sparse or entirely lacking, species inhabit more open woodland and rocky habitats. Since these habitats are more widespread and less fragmented, inland species usually have much wider ranges. While the precise patterns of spatial differentiation and local adaptation of populations in dryer areas of the Kimberley are currently not well understood (Solem, 1981a; Cameron, 1992; Köhler, 2010a), it is postulated that while in general the species diversity in xeric habitats is much lower, species ranges are larger overall.

Field work during the Kimberley Island Survey has recovered up to thirteen camaenid species per island (i.e., Boongaree Island where all species were found in sympatry). The average number of species per island across all 25 surveyed islands along the coast line was much lower (4.0). These figures are comparable to a maximum of 12.5 and an average of 3.7 camaenid species found per rainforest patch on the mainland (Solem, 1991). Solem

& McKenzie (1991) demonstrated that in land snails of the Kimberley patterns of species richness are correlated with attributes of rainfall, temperature and substrate. Rainfall patterns vary greatly along the coastline of the Kimberley and different islands may receive on average between > 600 mm and > 1,200 mm of precipitation per annum (McKenzie, 1991). The species richness of islands correlates well with the clinal variation of annual rainfall. Islands within the > 1200 mm isohyets support on average 6.4 species, while islands receiving between 1,000 and 1,200 mm support 4.3 species and those with less than 1,000 mm only 2.0 species.

Species found in sympatry predominantly belong to different genera while in turn congeners mostly occur in allopatry. There are few exceptions in *Amplirhagada* and ***Kimberleytrachia*** with up to three species from each genus occurring in sympatry on Boongaree Island and two on some other islands. The dominance of allopatric distributions suggests that spatial separation has been the main factor driving speciation in the Kimberley Camaenidae. It has been argued by Cameron (1992) for camaenids from the Kimberley mainland that allopatry in these snails may partly be caused or maintained by competition and ecological exclusion resulting in geographical replacement of species with similar ecological adaptations. Whether allopatric speciation in the island species is driven by dispersal from island to island, vicariance events relating to sea level changes or ecological replacement as suggested for the mainland species, remains to be tested.

ACKNOWLEDGEMENTS

This work has been conducted as part of the Kimberley Island Survey of the Western Australian Department of Environment and Conservation (DEC), a project jointly funded by the Commonwealth of Australia and the Western Australian Government. I owe a debt of gratitude to Marlene Vial, Sue Lindsay and Martin Püschel for their help with sample processing, SEM work, anatomical drawings and photography, to Shirley Slack-Smith, Corey Whisson (WAM), Jochen Gerber (FMNH), Alison Miller and Janet Waterhouse (AM) for most effectively handling extensive loans from or to their respective museums and to Winston Ponder and Norm McKenzie for encouraging me to work with Kimberley camaenids. I wish to thank four reviewers as well as Gene Coan for carefully reading a former version of the manuscript. Their comments were helpful to improve the quality of this paper. Special thanks are also due to Tom Vigilante and Thomas Saunders (Kimberley Land Council) who liaised with Traditional Owners for permission to use Indigenous names and provided linguistic advice. Eventually, thanks are also due to everybody who contributed to the successful implementation of the Kimberley Island Survey. This includes traditional landowners of the Malaya, Dambimangari, and Bardi-Jawi people, the Kimberley Land Council as well as staff and associates of DEC, the Australian Museum and Western Australian Museum. Janet Oobagooma, Heather Umbagai, Jack Karadada, Basil Djanghara, Sylvester Mangolamara and Sylvia Djanghara provided advice on indigenous language names.

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Revised ms. accepted 4 June 2011

MALACOLOGIA, 2011, 54(1–2): 407–427

REINSTATEMENT OF THE FISSURELLID SUBFAMILY HEMITOMINAE, WITH THE DESCRIPTION OF NEW GENERA, AND PROPOSED EVOLUTIONARY LINEAGE, BASED ON MORPHOLOGICAL CHARACTERS OF SHELL AND RADULA (GASTROPODA: VETIGASTROPODA)

James H. McLean

Natural History Museum of Los Angeles County,
900 Exposition Blvd., Los Angeles, CA 90007-4057, U.S.A.;
jmclean@nhm.org

ABSTRACT

The fissurellid subfamily Hemitominae Kuroda, Habe & Oyama, 1971, has been synonymized under the subfamily Emarginulinae by recent authors. Here it is redefined and characterized by a shell with either a short slit and selenizone, or a small notch without selenizone, and a radula synapomorphy, in which the rachidian and adjacent lateral teeth are of nearly the same size, the central field partitioned by a "transverse ridge." A generic review treating nine genera, including three new genera, is provided.

Three new genera – ***Hemimarginula***, ***Octomarginula***, and ***Variegemarginula*** – are considered basal, differing from the Mesozoic stem genus *Emarginula* Lamarck, 1801, in lower profile and by the shorter slit and radula synapomorphy. The genus *Montfortula* Iredale, 1915, is also basal, having a selenizone and notch visible in anterior view. The earliest basal member of the hemitomine lineage is the extinct *Loxotoma* Fischer, 1885, which arose in the Late Jurassic. Derived genera are *Montfortia* Récluz, 1843; *Montfortista* Iredale, 1929; and *Hemitoma* Swainson, 1840, which lack the slit and selenizone but have a notch in anterior view. *Montfortulana* Habe, 1961, and *Clypidina* Gray, 1847, are further derived, with the transverse ridge replaced by clumped pustules.

Instead of progressing to a shell form with an excurrent foramen at the apex (as in the derived emarginuline genera *Puncturella* Lowe, 1827, and *Diodora* Gray, 1821), this lineage reduces the prominence of the slit and leads to an imperforate shell that resembles the shell of other limpet groups.

My concept of the Hemitominae differs from that of the recent molecular phylogeny of Fissurellidae (Aptikis et al., 2011), which was poorly resolved, principally because it sequenced species of four rather than nine genera here determined as Hemitominae.

Key words: Fissurellidae, Hemitominae, subfamily classification, phylogeny, radular morphology, shell morphology, fossil record.

INTRODUCTION

The family Fissurellidae is the least understood of the vetigastropod limpet groups. There have been only three attempts to treat all species, that of G. B. Sowerby II (1862), which was continued by A. Adams (1863), that of Pilsbry (1890), who copied original descriptions and illustrations, and that of Thiele (1917), who also provided copies of the early illustrations. Most subsequent work has been done by authors of faunistic accounts, who have managed to determine local species (e.g., Wilson, 1993; Higo et al., 1999).

Previous efforts at subfamily-level classification are those of Pilsbry (1890): Emarginulinae, Fissurellinae, and Fissurellidinae; Thiele (1929): Emarginulinae, Fissurellinae; Wenz (1938): Emarginulinae, Diodorinae, Fissurellinae; Knight et al. (1960): Emarginulinae, Diodorinae, Fissurellinae; Christiaens (1977): Fissurellinae, Fissurellidinae, Emarginulinae, Scutinae; McLean (1984c): Emarginulinae, Fissurellinae; Christiaens (1991): Fissurellinae, Emarginulinae, Fissurellidinae, Hemitominae, Scutinae; McLean & Geiger (1998): Emarginulinae, Fissurellinae; Warén & Bouchet (2005): Fissurellinae, Emarginulinae (with other taxa as tribes under Emarginulinae).

The two-subfamily classification of Thiele, McLean, McLean & Geiger, and Warén &

Bouchet is based on a radula dichotomy that separates the Cenozoic-arising Fissurellinae from the Triassic-originating Emarginulinae. Further subdivisions of the Emarginulinae, whether as additional subfamilies or tribes, are here considered to be paraphyletic until the genera are better known. Genera that share features in common are recognized in my previous papers (McLean, 1984b, 1984c; McLean & Geiger, 1998) as "generic groups." Here, however, I attempt to show that in the Jurassic-appearing Hemitominae, there is a radula synapomorphy and synapomorphic shell morphology within the lineage, the recognition of which increases the number of monophyletic subfamilies to three.

The subfamily Hemitominae Kuroda, Habe, & Oyama, 1971, has had a checkered history of acceptance during the 40 years subsequent to its proposal. It was not recognized for the fissurellid text for *Fauna of Australia* by Hickman (1998). In the text for the Vetigastropoda of the *Working Classification of the Gastropoda* by Warén & Bouchet (2005), Hemitominae was synonymized without comment under the tribe Emarginulini of Emarginulinae.

Historical Chronology of Hemitominae

Thiele (1917, 1929) used only two genera – *Hemitoma* Swainson, 1840, and *Clypidina* Gray 1847 – for species treated here. He figured the radula for the type species of each genus, but gave no information on the radula of other species. Thiele (1917) also assigned 23 previously described species to *Hemitoma* and 17 described species to *Clypidina*. However, Thiele (1917) was prescient enough to recognize the affinity of many species of divergent shell morphology that are here assigned to additional genera based on shell morphology. Both genera were assigned by Thiele to the Emarginulinae.

The original proposal of Hemitominae (Kuroda, Habe & Oyama 1971: 10) is repeated here: "The shell conically elevated, cup-shaped, solid. Surface with distinct radial ribs and a short notch anteriorly. Radula has the rachidian tooth of ellipsoidal shape." This was lacking in detail for the radula, but at least mentioned that the notch is short.

Golikov & Starobogatov (1975: 185) overlooked Kuroda, Habe & Oyama, 1971, and separately proposed Hemitomidae as a full family among three families in the superfamily Fissurellacea, justified without a diagnosis in a footnote: "We find the differences from Emarginulidae and Fissurellidae important and our reasoning on the evolution of the Scutibranchia leads us to the conclusion that the Hemitomidae originated from other bellerophon-like ancestors." These remarks completely failed to characterize the group. In the same paper, Golikov & Starobogatov had speculated that fissurellids were descendants of Paleozoic bellerophontids, a concept further explored by McLean (1984a). However, the ancestral derivation of the Fissurellidae is still an open question, because the fossil record does not provide intermediate shell morphologies having the slit and selenizone.

Hickman (1980: 285) provided the first SEM illustrations of the radula of *Hemitoma octoradiata, Montfortula rugosa*, and *Clypidina notata*. "A more striking contrast is illustrated by the rachidian tooth within the superfamily Fissurellacea (the keyhole limpets and their allies). It is much reduced in development and characteristically asymmetrical in form. In the subfamily Fissurellinae, the asymmetrical cusp is narrow and rounded; in the subfamily Hemitominae, it is broader and denticulate and less obviously asymmetric; and in the subfamily Diodorinae, it is broad and simple. These morphologies are constant enough to be diagnostic at the subfamily level, although tooth proportions may vary considerably from one species to another or even among individuals from one population to another." These comments were incomplete as a diagnosis for Hemitominae, but Hickman did note that the rachidian tooth is less asymmetric than in Diodorinae and Fissurellinae.

Christiaens (1987, 1991) did not study radulae with SEM; he followed the example of Thiele (1917) and placed all species in *Hemitoma* or *Clypidina,* with the then-available taxa as subgenera; both genera were assigned by Christiaens (1987) to the Emarginulinae. However, he later (1991) reversed himself and recognized Hemitominae.

Herbert (1987: 1) remarked: "*Hemitoma* is here maintained within the Emarginulinae although several authors have elevated the taxon to subfamilial (Kuroda, Habe, & Oyama 1971; Hickman 1980) and even familial rank (Golikov & Starobogatov 1975). No reasons, however, have been given and such a high ranking at present seems unwarranted. The *Hemitoma* – *Clypidina* group appears to contain *Emarginula*-like forms adapted to a harsher intertidal and shallow water environment, largely in tropical to warm temperate regions." Herbert & Kilburn (1986) and Herbert (1987) did not examine hemitomine radulae with SEM. Herbert (1987: 1) noted that Hickman (1980) had illustrated "a pronounced 'transverse ridge' situated in the centre of the exposed face."

Herbert recognized *Hemitoma* and *Clypidina* (with subgenera), further stating that "… it is evident that a worldwide revision of the genus at subgeneric and specific level is required. The great variability of many species has given rise to a relatively large number of names, some of which will doubtless prove to be synonyms."

McLean & Geiger (1998) provided a phylogenetic analysis of selected genera of Emarginulinae, based on shell and radular characters. Their summary cladogram placed *Diodora* of the sometimes recognized Diodorinae within Emarginulinae. A review by McLean of hemitomine genera was anticipated to follow, which explains why the hemitomine genera were not mentioned by Geiger & McLean. This is therefore the culmination of that plan.

Initial work on the molecular phylogeny of Fissurellidae has just been published (Aktipis et al., 2011). Subfamilies recognized were Emarginulinae, Diodorinae, Fissurellinae, and Hemitominae (the latter of differing composition from that proposed here). A detailed critique of their work is given in the discussion section.

The objective here is to define additional genera and provide morphological details and comparisons for the shell and radula of all the recognized hemitomine genera, which will enable future efforts at phylogenetic analysis to be based on a more complete understanding of the genera and assigned species.

METHODS

For purposes of simplification and clarity, this effort is limited to analysis of characters of the shell and radula. Diagnostic morphological characters mentioned here for nine living genera and one fossil genus are summarized in Table 1. Terminology used here (e.g., evolutionary, lineage, basal, transitional, derived, etc.) is used in a traditional, non-restricted manner, without the implication that a complete phylogenetic analysis has been performed to produce a computer generated tree of my own.

Except for a few SEM illustrations provided by Hickman (1980, 1981), previous illustrations of hemitomine radulae have been line drawings (e.g., Thiele, 1917, 1929; Christiaens, 1987; Herbert, 1987). SEM illustrations for the radula of the type species or other species of the nine recognized genera are provided here. Prior to beginning my SEM work, a number of stained whole mount preparations of radulae were made. These whole mount preparations are also cited because they increase the number of examined specimens, and provide further evidence for the assumption that the radula is consistent in each genus. Voucher specimens of illustrated shells, or shells from which radulae were extracted for SEM preparations, are labeled in the LACM collection.

TABLE 1. Summary of diagnostic character states for radula and shell of hemitomine genera. Basal genera have a short slit and selenizone; derived genera have lost the slit and selenizone. Non-applicable character states are left blank. *Emarginula* is the outgroup (subfamily Emarginulinae). *Loxotoma* is here regarded as the oldest member of Hemitominae (Upper Jurassic of Europe).

Genus	Transverse ridge of radula	Shell profile	Primary ribs/ secondaries	Slit length	Selenizone	Notch in anterior view	Projecting anterior rib	Symmetry
Emarginula	lacking	varies	alternating	long	narrow			normal
Loxotoma	(fossil)	medium	alternating	short	broad			deflected
Hemimarginula	present	varies	irregular	short	narrow			normal
Octomarginula	present	low	eight	short	broader			normal
Variegemarginula	present	high	alternating	short	narrow			normal
Montfortula	present	medium	alternating		narrow	V-shaped		varies
Montfortia	present	high	irregular			V-shaped		normal
Montfortista	present	high	irregular			V-shaped	strong	varies
Hemitoma	present	low	eight			low		slight
Montfortulana	pustules	low	alternating			low		deflected
Clypidina	pustules	medium	alternating			lacking		normal

Shells of all genera treated here are illustrated for the exterior, interior and left side views. The notch of *Montfortula*, *Montfortia*, *Montfortista,* and *Hemitoma* best shows in a view of the anterior slope of the shell. Although this view is usually not provided in illustrations of limpets, it is provided here in order to show the extent of the notch (or its absence), and how its presence is not revealed in a standard exterior shell view.

Good illustrations for type species and other familiar species are also provided in the following regional identification manuals – Western Atlantic: Abbott (1974), De Jong & Coomans (1988); Eastern Pacific: McLean in Keen (1971); India: Subba Rao (2003); Japan: Higo et al. (1999), and for shell illustrations Sasaki in Okutani (2000); Philippines: Poppe (2008); Australia: Wilson (1993). Some species of the Indian Ocean were depicted by Herbert (1987); species of the Red Sea were illustrated by Christiaens (1989).

This effort is a generic level review; I am unable to verify the identifications of some previously illustrated species, but in the absence of a monographic treatment, I am assigning a few undetermined specimens or citing figures of other authors in order to demonstrate that all genera except for *Clypidina* are represented by additional species.

Museum abbreviations: LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History.

SYSTEMATICS

Subfamily Hemitominae
Kuroda, Habe & Oyama, 1971

Hemitominae Kuroda, Habe, & Oyama, 1971: 10. Type genus *Hemitoma* Swainson, 1840.

Hemitomidae Golikov & Starobogatov, 1975: 185. Not diagnosed; this is an objective synonym of Hemitominae Kuroda, Habe, & Oyama, 1971.

Revised Diagnosis

Body not greatly exceeding size of shell. Mature shell with nearly central apex, lateral profile low to elevated with slight posterior overhang of the apes. Sculpture of primary and secondary radial ribs. Anterior rib either split by short slit preceded by selenizone (= slit band) originating at apex; or, with slit only in juvenile stage, and anterior rib lacking selenizone, with strong to imperceptible notch at margin. Shell interior with narrow groove connecting notch or slit to apex. Muscle scar with hooks; area within muscle scar shaped like an inverted mushroom.

Rachidian tooth and three pairs of lateral teeth of nearly equal size; fourth pair of lateral teeth reduced; rachidian and lateral teeth with raised transverse ridge on inner face, or with similarly aligned, massive pustules on face of tooth shaft, lower part of shaft broader than upper; pluricuspid teeth with one or two main prongs, with smaller divisions on either side; marginal teeth like those of other fissurellids.

Shell Comparisons

Genera with the slit (the new genera ***Hemimarginula***, ***Octomarginula***, and ***Variegemarginula***) resemble the genus *Emarginula* in having a selenizone that precedes the slit, but the slit in all of these new genera is always much shorter than in the emarginuline genus *Emarginula,* and the lateral profile is usually lower than that of *Emarginula*. The established genus *Montfortula* has a narrow selenizone, but the slit does not show in dorsal view and is reduced to a notch visible in anterior view. In *Montfortia*, *Montfortista*, and *Hemitoma*, the selenizone is present in larval shells, but there is no selenizone in large shells, and a notch shows in anterior view. The notch is weak in *Montfortulana* and lacking in *Clypidina*. All genera, including those that lack the slit, have a low apex in central position or posterior to center; all have a groove on the shell interior that connects either the notch or slit to the shell apex. These shell characters are sufficiently reliable to establish the affinity of specimens known only from shells, enabling the assignment of both living and fossil specimens.

Shells of all hemitomine genera differ from emarginuline genera of low profile that have bodies larger than the shell (e.g., *Emarginella* Pilsbry, 1891*; Scutus* Montfort, 1810*; Tugali* Gray, 1843) in having the interior groove that connects the slit or notch to the apex.

Radula Comparisons

Herbert (1987: 1) introduced the term "transverse ridge," for the mid-shaft partition that shows in the central field of the hemitomine radula, both in drawings and SEM illustrations (Figs. 1–10). This is a diagnostic, synapomorphic character that is unique in the Fissurellidae. In two genera (*Montfortulana* and *Clypidina*), the transverse ridge is replaced by a field of sharply projecting pustules (Figs. 11, 12); precursors to these pustules also show in the higher magnification images of ***Hemimarginula*** (Fig. 2) and ***Variegemarginula*** (Fig. 5), so these pustules are considered a derived character state for the transverse ridge in *Montfortulana and Clypidina*. These pustules for *Clypidina* were first illustrated by Hickman (1980: fig. 6a).

The hemitomine radula also differs from that of the Emarginulinae and that of the Fissurellinae in having the rachidian and lateral teeth of nearly equal size. The pluricuspid tooth is sufficiently large that it causes the radular asymmetry that characterizes both Emarginulinae and Fissurellinae, although the asymmetry is not as extreme as in either the Emarginulinae and Fissurellinae.

Thiele (1917, 1929) figured radula drawings of both *Hemitoma* (with the transverse ridge) and *Clypidina* (lacking the transverse ridge), a striking dichotomy, which could thereafter have served a purpose as long as the subgenera of subsequent authors were to be consistent with this distinction. However, the first available and useful taxon *Montfortula* was incorrectly assigned by Thiele himself (1929) to *Clypidina*, followed by Christiaens (1973, 1991), both of whom did not realize that *Montfortula* has a radula like that of *Hemitoma* rather than *Clypidina*.

Justification for Recognition of Hemitominae

The shell has a short slit or notch and the interior has a corresponding excurrent groove, unlike that of other fissurellids. The radula is synapomorphic for Hemitominae, having teeth of the central field (rachidian tooth plus lateral teeth) of similar size, with a prominent “transverse ridge” or pustules on the shaft, the teeth sufficiently cusped to have some role in feeding. This is unlike the emarginuline or fissurelline radula, in which the rachidian and laterals are not similar, do not have the transverse ridge, and are generally uncusped in species of large shell size.

Key to living hemitomine genera, with type species (*) and distribution

I. Radula with transverse ridge of central field
II. Radula with transverse ridge replaced by pustules

I. Radula with transverse ridge

A. With short slit and long selenizone within major anterior rib

Hemimarginula n. gen. Radial ribs markedly alternating in size [**dentigera*, Caribbean]. Other species in Caribbean and Indo-Pacific.

Octomarginula n. gen. Apex central, profile low, radial ribs of eight strong primary ribs [**ostheimerae*, Caribbean]. Other species in tropical eastern Pacific and Indian Ocean.

Variegemarginula n. gen. Apex recurved, radial ribs only slightly alternating in size [**variegata*, Indo-Pacific]. Other species are known from the Indo-Pacific.

B. With selenizone, but notch visible only in anterior view

Montfortula Iredale, 1915. Apex central, slightly recurved; radial ribs narrow, with low notch and narrow selenizone [**rugosa*, southeastern Australia]. Other species are known from the tropical Indo-Pacific.

C. Selenizone lacking, notch visible in anterior view

Montfortia Récluz, 1843. Apex raised and recurved, ends of shell raised; radial ribs with 3 enlarged anterior primary ribs [**australis*, Australia]. Other species in western Atlantic and eastern Pacific.

Montfortista Iredale, 1929. Apex raised and recurved, ends of shell raised; radial ribs with 3 enlarged anterior primary ribs, the central rib greatly extended anteriorly [**excentrica*, Indo-Pacific]. Other species in Indo-Pacific.

Hemitoma Swainson, 1840. Apex central, not recurved; radial ribs of eight enlarged primary ribs, secondaries reduced [**octoradiata*, Caribbean]. Another species in Indian Ocean.

II. Radula with reduced transverse ridge; notch lacking, with interior groove only

Montfortulana Habe, 1961. Apex posterior to center, radial ribs narrow, alternating primaries and secondaries, with faint notch and strong channel deflected to right [**sulcifera*, Indo-Pacific]. Other species are from the Indo-Pacific.

Clypidina Gray, 1847. Apex central, low in profile and not recurved; radial ribs narrow, black at crest, notch highly reduced [**notata*, Sri Lanka and India]. Monotypic.

REVIEW AND DESCRIPTIONS OF GENERA

I. Radula with transverse ridge

Group A – Genera with short slit and selenizone

Genus **Hemimarginula** n. gen.
(Figs. 1, 2, 13–18)

Type species: *Emarginula dentigera* Heilprin, 1889 (Fig. 13), previously misdetermined as *pumila* A. Adams, 1851 (see below). Other figures of type species: Abbott, 1974: fig. 41, as *pumila*; De Jong & Coomans, 1988: pl. 29, fig. 3, as *pumila*. Caribbean.

Shell (Figs. 13–18): Profile low to moderately elevated; primary radial rib count varies, each primary separated by secondary ribs of lesser size. Slit short, slit and selenizone within bifurcated anterior cord, flanked by two primary cords to make a raised anterior slope; color brown with lighter broad cords. Interior with a channel of selenizone width leading to apex.

Radula (Figs. 1, 2, *dentigera*): Rachidian of same width as laterals. Teeth of central field with transverse fold that forms a thickening above, with pustules below the ridge; pluricuspid with projecting prongs, with one short division on the inner side and two smaller divisions on outer side; large lateromarginal plate on outer side of pluricuspid.

Other Examined Whole Mount Preparations: *H. pileum*, LACM 177645; *H. pumila*, LACM 65-26.26.

Comparisons: *Hemimarginula* is usually characterized by the three anterior primary ribs that are broadly expanded, whereas in *Emarginula* the primary ribs remain narrow, with smaller secondary ribs added. Shells of *Emarginula* are usually white; whereas those of ***Hemimarginula*** may be brown with lighter colored primary cords.

Species: The three Caribbean species in Figures 13–15 have been confused by Farfante (1947) and by Abbott (1974). The first figure of the older name *pumila* A. Adams, 1851, provided by A. Adams & G. B. Sowerby II (1863: pl. 12, fig. 80), is oval in outline like that of Figure 14. Two subsequent names of Heilprin (1889) were confused by Abbott (1974). Figure 13 is here determined as a match for *dentigera* Heilprin, 1889, and Figure 15 as a match for *pileum* Heilprin, 1889, which has a higher profile, according to the original measurements.

Figure 17 shows an undetermined species of ***Hemimarginula*** from northwestern Madagascar, in which the apex is more anterior and the slit is a little shorter than that of the type species.

The Japanese species treated as *Emarginula biangulata* G. B. Sowerby III, 1901, by Sasaki in Okutani (2000: pl. 23, fig. 18) is clearly a member of *Hemimarginula* because of its very short slit and three stronger anterior ribs, the selenizone within the anterior rib; this is matched here by Figure 16.

Christiaens (1987) illustrated three species from the Red Sea that are here assigned to *Hemimarginula*: *subrugosa* Thiele, 1916 (figs. 68, 69); *modesta* H. Adams, 1872 (fig. 71), and *simpla* Christiaens, 1987 (fig. 43); his figures show the short slit, selenizone and the two adjacent anterior primary cords. Figure 18 here is a match for *subrugosa* of Christiaens, 1987.

Distribution and Occurrence: Recent members of the genus are known from the Caribbean and the Indo-Pacific from Japan to the Red Sea. This genus is characteristic of shallow water in tropical regions and occurs on under sides of rocks in the intertidal zone. *Hemimarginula* is a speciose genus of small-shelled species; many shells recovered from shell grit remain unidentified in the LACM collection.

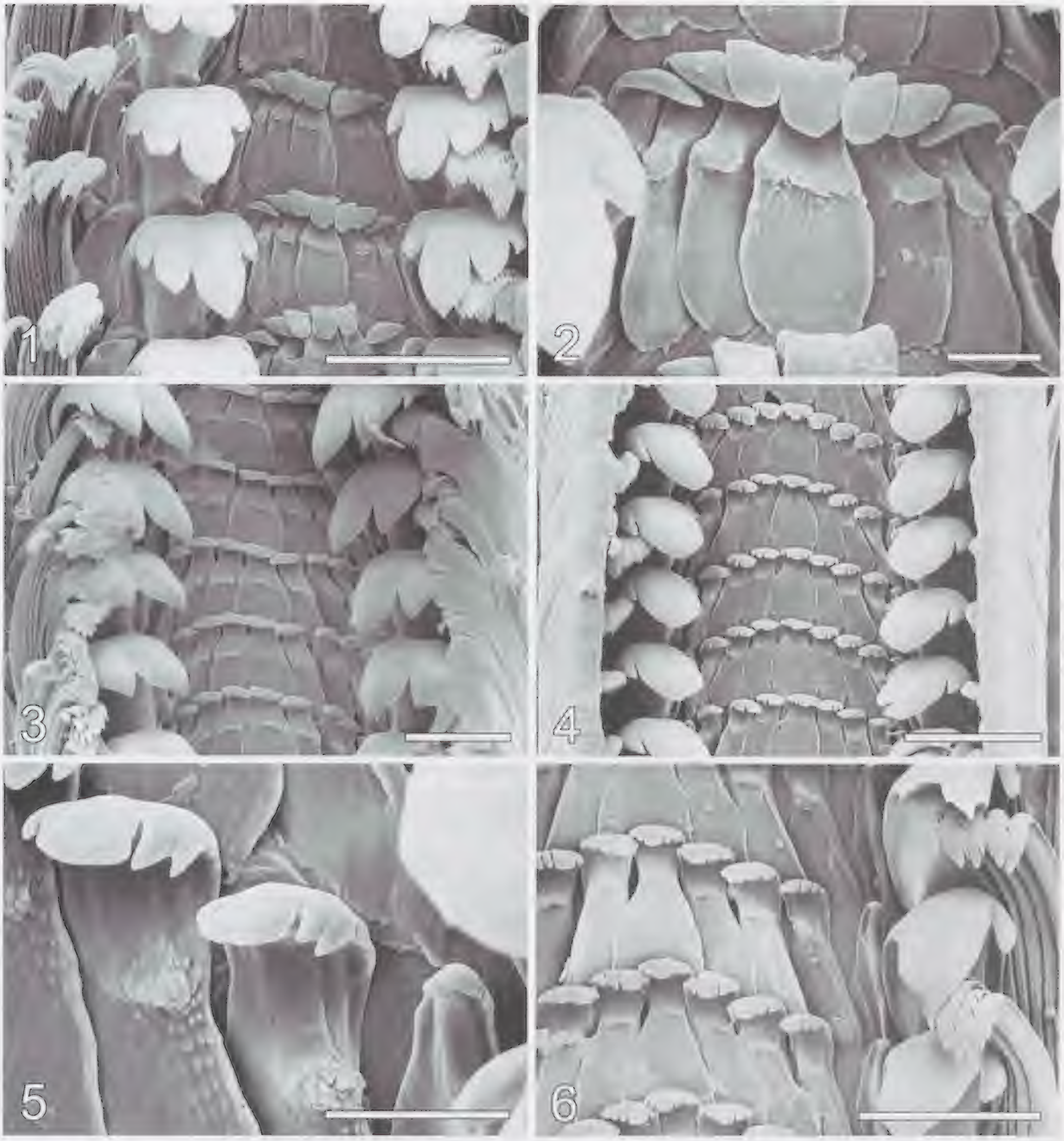
Fossil Record: The genus may be traced to the Pleistocene Caloosahatchee Formation of Florida with *Emarginula pilsbryi* Dall, 1892. Dall's species was also figured by Olsson & Harbison (1953: pl. 63, fig. 8).

Taxonomic History: Only Thiele (1917: 114) recognized the hemitomine affinity of the species *pumila* A. Adams, 1851, by placing it in *Hemitoma*. Farfante (1947: 108), did not cite Thiele (1917), but remarked that the type species was included by her in *Emarginula* "with some doubt." Christiaens (1987) was the only recent author to understand the affinity of this group; however, he did not propose a genus distinct from *Hemitoma*. *Hemimarginula* has an overall aspect more like that of *Hemitoma* than of *Emarginula*. Hence, the derivation of the name.

Genus **Octomarginula** n. gen.
(Figs. 3, 19–22)

Type species: *Emarginula ostheimerae* Abbott, 1958 (Figs. 19, 20) Caribbean. Other figure: De Jong & Coomans, 1988: pl. 29, fig. 7.

Shell (Figs. 19, 20, *ostheimerae*; 21, 22, *natlandi*): Profile of moderate height; apex central, not strongly projecting. Radial sculpture of eight primary ribs, secondary ribs of much lesser strength; each primary rib tending to be subdivided with size increase; concentric ribs

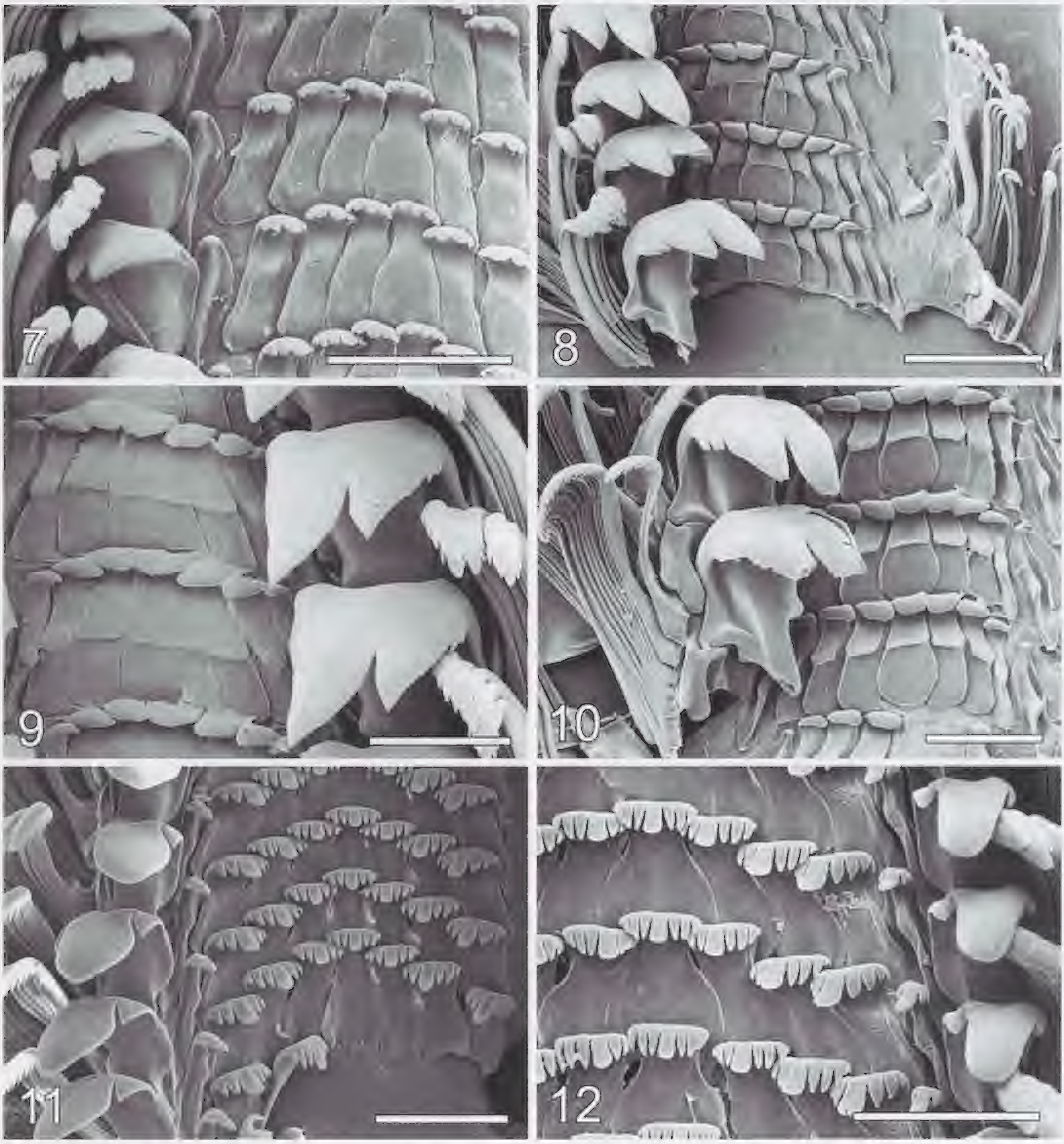


FIGS. 1–6. Radula morphology of hemitomine genera. FIG. 1: *Hemimarginula dentigera*, Portobelo, Caribbean Panama, 2 m. LACM 70-19.15. Scale bar = 100 µm; FIG. 2: Enlarged view of same. Scale bar = 20 µm; FIG. 3: *Octomarginula natlandi*, N side Santa Elena Peninsula, Ecuador, 9 m. LACM 66-114.26. Scale bar = 50 µm; FIG. 4: *Variegemarginula variegata*, S side Lizard Island, Queensland, Australia, intertidal. LACM 79-53.39 Scale bar = 100 µm; FIG. 5: Enlarged view of same. Scale bar = 20 µm; FIG. 6: *Montfortula rugosa*, Long Reef, Sydney, New South Wales, Australia, intertidal. LACM 79-58.7. Scale bar = 100 µm.

strong, broadly spaced. Short slit at margin, selenizone moderately broad, within anterior-most rib.

Radula (Fig. 3, *natlandi*): Rachidian of same width as laterals. Teeth of central field with transverse fold that forms a thickening above, pluricuspid with projecting prongs, with one division on the inner side and two on the outer side; large lateromarginal plate on outer side of pluricuspid.

Other Examined Whole Mount Preparations: *O. natlandi*, LACM 68-41.82.



FIGS. 7–12. Radula morphology of hemitomine genera, continued. FIG. 7: *Montfortula pulchra*, Guimeras Island, Iliola Province, Philippines, intertidal. LACM 74668. Scale bar = 100 µm; FIG. 8: *Montfortia emarginata*, Montego Bay, Jamaica, 1 m. LACM 65-26.24. Scale bar = 20 µm; FIG. 9: *Montfortia panhi*, Nusa Dua, Bali, Indonesia, intertidal. LACM 86-164.51. Scale bar = 100 µm; FIG. 10: *Hemitoma octoradiata*, Montego Bay, Jamaica, intertidal. LACM 65-26.25. Scale bar = 100 µm; FIG. 11: *Montfortulana* sp., Orofara, Mahina, Tahiti, French Polynesia, exposed intertidal basalt. SBMNH 83702. Scale bar = 100 µm; FIG. 12: *Clypidina notata,* Tangalla Bay, Sri Lanka, intertidal. LACM 83-5.1. Scale bar = 100 µm.

Comparisons: Shell sculpture of the major ribs is similar to that of *Hemitoma*, except that the anterior primary rib envelops a selenizone and there is a short notch in advance of the selenizone. The selenizone is broader than that of *Hemimarginula*.

Species: Western Atlantic, the type species *ostheimerae* Abbott, 1968. A large shell is shown in Figure 19; all previous illustrations have been of small specimens like that of Figure 20.

The Panamic species previously known as *Hemitoma natlandi* Durham, 1950 (Figs. 21–22; McLean in Keen, 1971: fig. 8), is here assigned to *Octomarginula* because it has a short slit and a selenizone comparable to that of the type species, and in having a central apex and a low number of primary ribs; small and large specimens are figured here.

The species *scutellata* Deshayes, 1863, from Reunion Island, Indian Ocean, as illustrated by Herbert (1987: figs. 1–5), is here assigned to *Octomarginula* because the illustrations clearly show a short slit and a somewhat broad selenizone.

The species from the Red Sea illustrated as *arabica* A. Adams, 1851, by Christiaens (1987: fig. 72) is here assigned to *Octomarginula*.

Distribution and Occurrence: Recent members of the genus are known from the Caribbean, the Panamic Province, and the Indian Ocean and Red Sea. Species of this genus occur in shallow water in the eastern Pacific and western Atlantic. It occurs on under sides of rocks in the intertidal zone; some specimens of *O. natlandi* are coralline encrusted and evidently live on exposed surfaces of rocks encrusted with coralline algae.

Fossil Record: *Octomarginula natlandi* was described as a Pleistocene species from the Gulf of California.

Taxonomic History: Previous authors have assigned the type species either to *Emarginula* (e.g., Abbott, 1958), or to a misunderstood concept of *Hemitoma* (e.g., Turner, 1959). The type species *O. ostheimerae* was incorrectly assigned to the synonymy of "*Hemitoma*" *emarginata*, by Turner (1959: 340), who did not examine or figure the holotype, which had been well illustrated by Abbott (1958).

Genus ***Variegemarginula*** n. gen.
(Figs. 4, 5, 23)

Type species: *Emarginula variegata* A. Adams, 1852 (Fig. 23). Indo-Pacific. Other figures: Sasaki in Okutani, 1990: pl. 22, fig. 2; Wilson, 1993: pl. 6, fig. 22).

Shell (Fig. 23, *variegata*): Profile elevated, apex recurved; gray and white or reddish, primary and secondary radial ribs of nearly similar size, ribs not scaly; often with two pairs of enlarged posterior ribs of lighter coloration; slit sharply defined, short and visible dorsally, selenizone narrow, formed between two half ribs.

Radula (Figs. 4, 5, *variegata*): Rachidian and laterals constricted below overhang, cutting edges with large median, subdivided by two prongs on the outer side and one on the inner side. Transverse ridge only slightly evident on rachidian, first three laterals with a "heel," on and below which there are projecting pustules. Fourth lateral narrow, with a medial ridge on face of shaft. Pluricuspid with broad, rounded main cusp, two deeply cut subdivision on outer side and one smaller one on inner side.

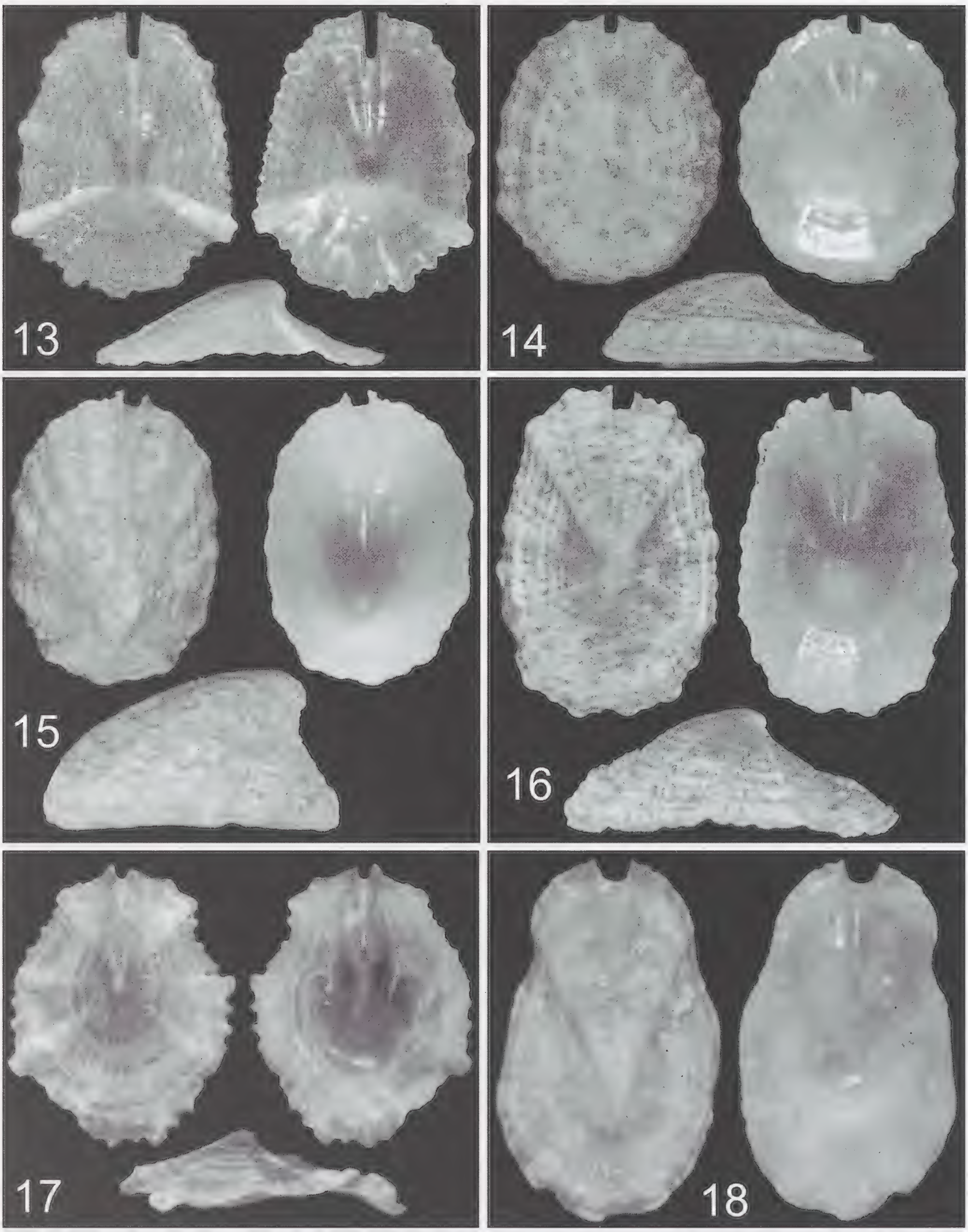
Other Examined Whole Mount Preparations: *V. variegata*, LACM 20783.

Comparisons: The shell of this genus differs from all species of true *Emarginula* in its variegated color pattern and in its short slit. This differs from the species of *Hemimarginula* in having uniformly fine radial ribs, not having the much broader primary ribs of that genus.

Species: *Variegemarginua variegata* has a high selenizone built by contributions from two half ribs. Two other species *punctata* A. Adams, 1852, and *foveolata fujitai* Habe, 1963, shown by Sasaki (in Okutani, 2000: pl. 22, figs. 1, 5) have similar sculpture and very short slits, so these species are provisionally assigned to the genus.

Distribution and Occurrence: The type species is common and widely represented in the LACM collection from Japan, the Philippines, and Queensland, Australia. Species occur in the Indo-Pacific only.

Fossil Record: Unknown.



FIGS. 13–18. Shells of ***Hemimarginula*** n. gen. FIG. 13: *H. dentigera*, Blauw Bay, W of Willemstad, Curacao, Netherlands Antilles, 30 m. LACM 74-28.6, 6.2 mm; FIG. 14: *H. pumila*, Montego Bay, Jamaica, shallow reef. LACM 65-26.26, 12 mm; FIG. 15: *H. pileum*, Big Pine Key, Florida, 1 m. LACM 177645, 6 mm; FIG. 16: *H. biangulata*. SE of Hedo Point, Okinawa, Japan, shell grit, 15 m, LACM 78-25.27, 7 mm; FIG. 17: *H.* sp., indet., Anpangorigina, Nosy Komba, Antseranana Province, off NW Madagascar, beach worn. LACM 89-56.3, 10.2 mm; FIG. 18: *H. modesta*, Southern Sinai Peninsula, Red Sea, Egypt, shell grit, 10–15 m. LACM 85-114.2, 5 mm.

Taxonomic History: Wilson (1993: 57, pl. 6, fig. 22) was the only previous author to have a clue about the affinity, by provisionally placing the type species in *Montfortula*.

Group B – With narrow selenizone, but notch visible only in anterior view

Genus *Montfortula* Iredale, 1915
(Figs. 6, 7, 24, 25)

Montfortula Iredale, 1915. Type species (original designation): *Emarginula rugosa* Quoy & Gaimard, 1834 (Fig. 22) Southeastern Australia. Other figures: Wilson, 1993: pl. 6, fig. 21.

Shell (Fig. 24, *rugosa*): Apex projecting, only slightly recurved, radial ribs numerous, alternating primaries and secondaries, notch visible only in frontal view. Short slit visible dorsally, under magnification it produces a selenizone in the middle of a primary rib that is slightly larger to accommodate the selenizone.

Radula (Fig. 6, *rugosa*): Rachidian and first three laterals with well marked transverse ridge at most constricted width of shaft; cusps with two to three deep cuts on either side; fourth lateral uncusped, with central ridge; pluricuspid with main overhang, concave on inner side, rounded on outer side; with lesser cusp on outer side; lateromarginal plate not exposed.

Previous SEM figures of radula *M. rugosa* – Hickman, 1980: pl. 1, figs. j, k; Hickman, 1981: figs. 8, 11, 12; Hickman, 1998: fig. L.

Other Examined Radula Preparations: Whole mounts, *M. rugosa*, LACM 68-81.3

Comparisons: *Montfortula* differs from the other basal genera *Hemimarginula*, *Octomarginula*, and *Variegemarginula* in not having a slit or notch visible in dorsal view. The narrow selenizone shows in dorsal view.

Species: The type species is common in southeastern Australia. This is the only species known in cool temperate waters; it has a lower profile than that of the tropical species currently assigned to the genus. There are no essential differences between the type species and other species (compare Figs. 6 and 7).

An unidentified species of *Montfortula* from the southern Japanese islands is figured here (Fig. 25); this species has the selenizone partially deflected to the right and it has larger and lighter colored posterior primary ribs than the type species. Note how similar large posterior ribs are also seen in certain species of *Hemimarginula* (Figs. 13, 17), and *Variegemarginula* (Fig. 23).

The Japanese species *Montfortula picta* (Dunker, 1860), as figured by Sasaki in Okutani (1990: pl. 25, fig. 41) is typical of tropical Indo-Pacifc species of higher profile; it is assigned to *Montfortula* because it has a short slit and selenizone within the anterior primary rib.

Also assigned is the species *brevirimata* Deshayes, 1862, *of* Herbert (1987: figs. 9–12, as *Clypidina*); it is assigned to *Montfortula* because it has a narrow selenizone within the large anterior rib.

Distribution and Occurrence: Southeastern Australia and tropical Indo-Pacific; *Montfortula* is not known in the Eastern Pacific and Western Atlantic.

Feeding: This species is a generalized grazer, feeding on fragments of microalgae and detritus. Analysis of stomach contents found large pieces of the algae *Ulva* and *Gracellaria*, as well as sponge spicules (Creese, 1978).

Taxonomic History: Thiele (1929: 34) placed *Montfortula* as a subgenus of *Clypidina*, which was subsequently followed by Christiaens (1977). However, the radula illustrations of Hickman (1980) established that the radula is comparable to that of *Hemitoma* rather than *Clypidina*.

Group C – Selenizone lacking, notch visible in anterior view

Genus *Montfortia* Récluz, 1843
(Figs. 8, 26)

Montfortia Récluz, 1843. Type species (subsequent designation, Iredale, 1915: *Emarginula australis* Quoy & Gaimard, 1834 [= *Emarginula subemarginata* Blainville, 1819]. Australia. Figure of type species: Wilson, 1993: pl. 6, fig. 34a–c.

Shell (Fig. 26, *emarginata*): Profile high, apex projecting, recurved, in some species deflected to right; sculpture coarsely clathrate, three strong anterior ribs; notch visible in frontal view in juvenile to mature stages, selenizone lacking in mature shell.

Radula (Fig. 8, *emarginata*): Rachidian and first two lateral teeth with strong transverse ridge; pluricuspid tooth with two large prongs and two weakly separated prongs on the outer edge.

Other Examined Radula Preparations: SEM for *Montfortia hermosa*, LACM 72-58; whole mount for *M. hermosa*, LACM 72-52.65; whole mount for *M. emarginata*, LACM 65-26.24.

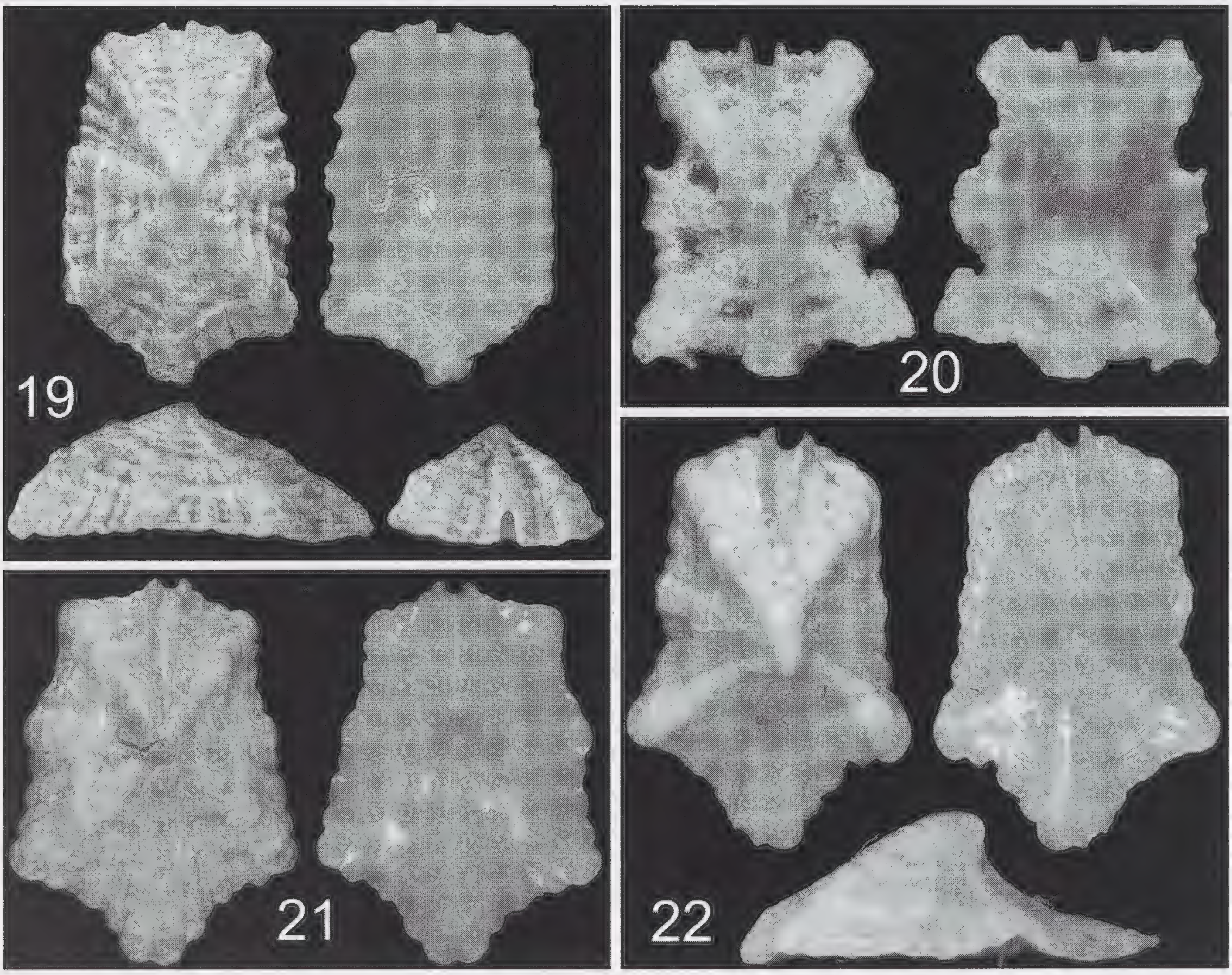
Comparisons: *Montfortia* is unlike other derived hemitomine genera in its three strong anterior ribs, the notch not visible in dorsal view of the shell. The anterior rib is not as projecting as it is in *Montfortista*. The radula of the species in the genera *Hemitoma* (Fig. 10) and *Montfortia* (Figs. 8, 9) is very similar.

Species: Australia (type species). Western Atlantic (Fig. 22, *emarginata* Blainville, 1825; Abbott, 1974, fig. 55). Eastern Pacific (*hermosa* Lowe, 1935; McLean in Keen, 1971: fig. 9).

Distribution and Occurrence: Southern Australia, Western Atlantic and Eastern Pacific, intertidal and shallow sublittoral zones.

Fossil Record: Early Pliocene of Jamaica. Illustrations of Woodring (1928: 40, figs. 6, 7) for his species *Hemitoma sclera* Woodring, 1928, are here considered indicative of the genus *Montfortia*, particularly because the ventral view shows the terminations of three strong anterior ribs.

Taxonomic History: Most recent authors have synonymized *Montfortia* and *Montfortista*, but



FIGS. 19–22. Shells of **Octomarginula** n. gen. FIG. 19: *O. ostheimerae*, large shell, reef off Doctors Cove, Montego Bay, Jamaica, 30 m. LACM 65-27.5, 12.2 mm; FIG. 20: *O. ostheimerae*, small shell, Western Dry Rocks, SW of Key West, Florida. LACM 87-104.1, 5.7 mm; FIG. 21: *O. natlandi*, large shell, Cuastocomate, Jalisco, Mexico. LACM 68-41.82, 14.3 mm; FIG. 22: *O. natlandi*, small shell, N side Santa Elena Peninsula, Ecuador, 9 m. LACM 66-114.26, 6.3 mm.

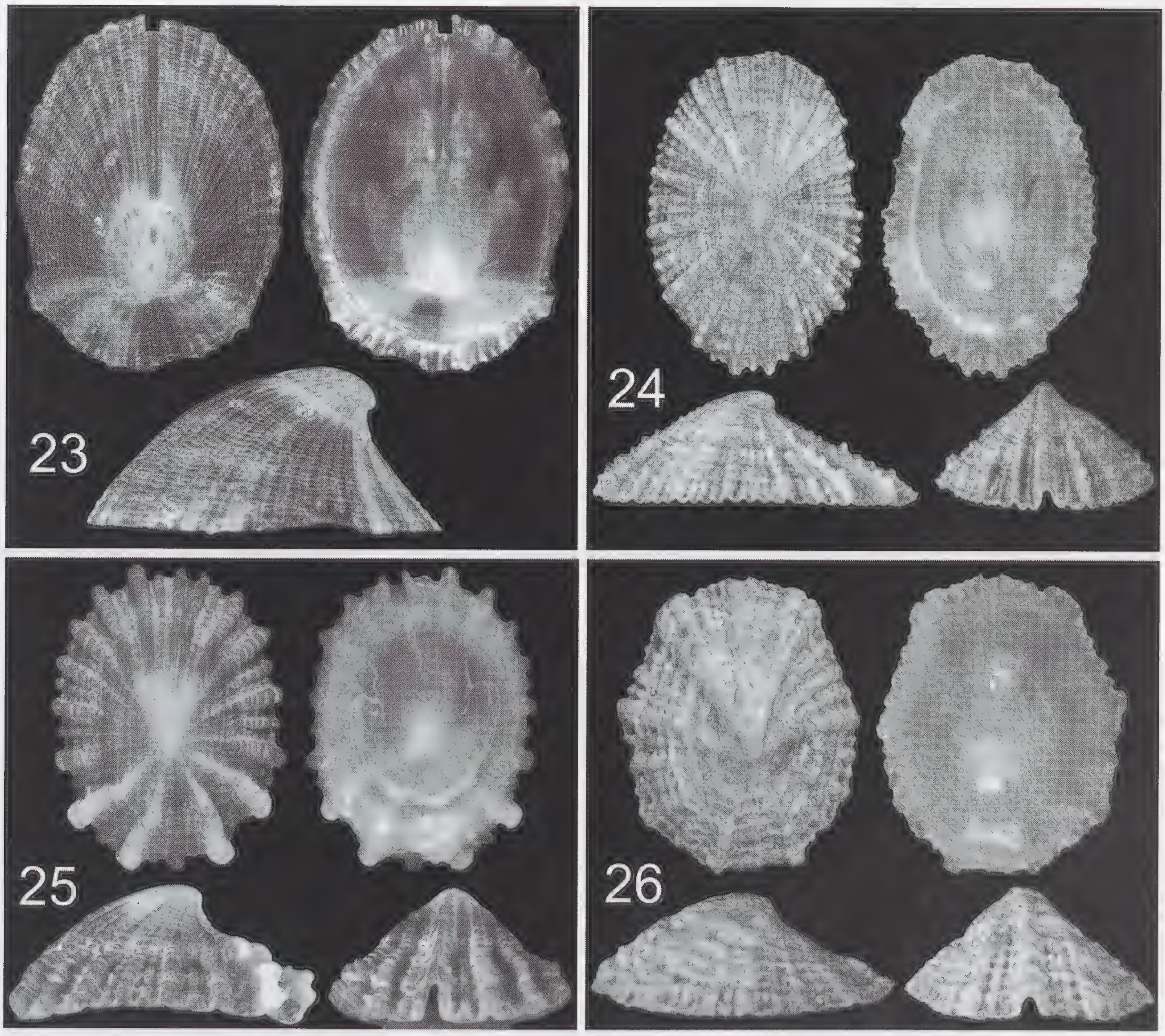
here they are recognized as distinct. Christiaens (1991) treated both taxa as synonyms of *Hemitoma*, but at least the radula for all three taxa is comparable.

Genus *Montfortista* Iredale, 1929
(Figs. 9, 27)

Siphonella Issel, 1869 (*non* Hagenow, 1851). Type species (monotypy): *Emarginula* (*Siphonella*) *arconatii* Issell, 1869 [= *Emarginula panhi* Quoy & Gaimard, 1834] (Fig. 27); Indo-Pacific. Other figure: Wilson, 1993: 57, text fig.

Montfortista Iredale, 1929. Type species (original designation): *Montfortia excentrica* Iredale, 1929. Northern Australia. Other figure: Wilson, 1993: 57, text fig.

Shell (Fig. 27, *panhi*): Profile high, apex projecting, recurved, in some species deflected to right; sculpture coarsely clathrate, three strong anterior ribs, the anterior rib strongly projecting beyond margin of shell; shells vary in position of juvenile stage with short slit; notch visible in frontal view in juvenile to mature stages, selenizone lacking in mature shell.



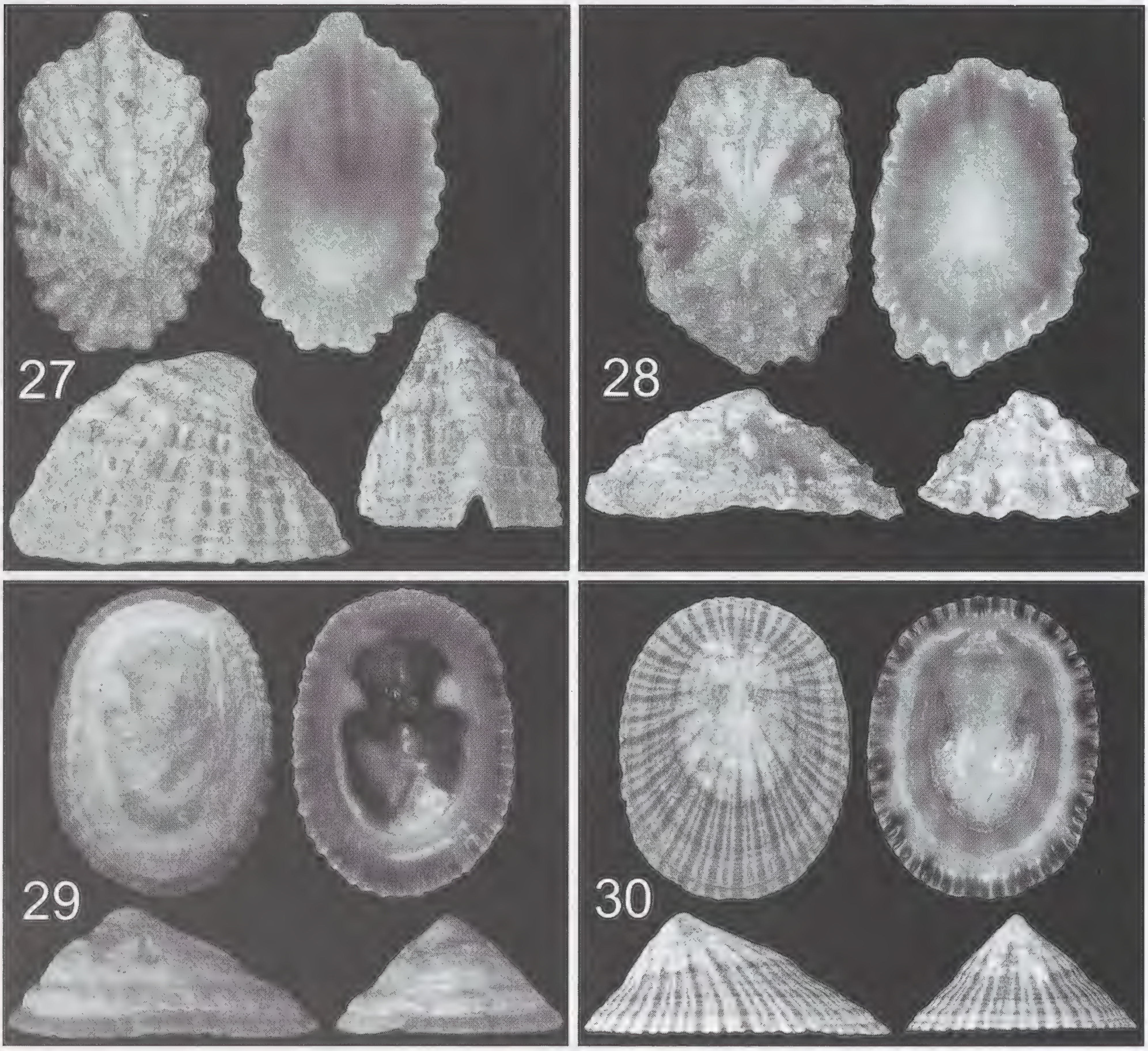
FIGS. 23–26. Shells of hemitomine genera, continued. FIG. 23: *Variegemarginula variegata*, Lizard Island, Queensland, Australia, intertidal. LACM 79-53.39, 8 mm; FIG. 24: *Montfortula rugosa*, Long Reef, Sydney, New South Wales, Australia, intertidal. LACM 79-58.7, 12 mm; FIG. 25: *Montfortula* sp., Oshima, Kagoshima Prefecture, Japan, LACM 25046, 11.5 mm; FIG. 26: *Montfortia emarginata*, Montego Bay, Jamaica, 1 m. LACM 65-26.24, 20.5 mm.

Radula (Fig. 9, *panhi*): Rachidian and laterals with well-marked transverse ridge; overhanging cusps continuous; pluricuspid with long, pointed inner cusp, and deeply separated outer cusp, with two very small accessory cusps.

Comparisons: *Montfortista* was intended for species that are strongly assymetrical, but the principal difference from *Montfortia* is that the anterior rib strongly projects beyond the anterior margin of the shell in dorsal view. Only by viewing the anterior slope of the shell is it possible to realize that there is a very strong notch.

Species: Australia (type species). Two Australian species that are assymetrical were assigned by Wilson (1993: 57): *panhi* (Quoy & Gaimard, 1934) and *excentrica* (Iredale, 1929; Wilson, 1994: 57 in text). For the Japanese species, Sasaki in Okutani (2000) included *panhi*, and *kirana* Habe, 1963, which have the strongly projecting anterior rib. For the Philippines, Poppe (2008) illustrated the species *kirana* Habe, 1963, and *panhi* Quoy & Gaimard, 1934.

One species illustrated by Sasaki in Okutani (2000: pl. 25, fig. 38) as *Montfortista oldhamiana* Nevill, 1869, has a different kind of



FIGS. 27–30. Shells of hemitomine genera, continued. FIG. 27: *Montfortista panhi*, Nusa Dua, Bali, Indonesia, intertidal. LACM 86-164.51, 15.2 mm; FIG. 28: *Hemitoma octoradiata*, Montego Bay, Jamaica, intertidal. LACM 65-26.25, 16.4 mm; FIG. 29: *Montfortulana* sp., Orofara, Mahina, Tahiti, French Polynesia, exposed intertidal basalt. D. L. Geiger 1587, 13.5 mm (exterior eroded); FIG. 30: *Clypidina notata*, Tangalla Bay, Sri Lanka, intertidal. LACM 83-5.1, 10 mm.

asymmetry in which there is a very strong rib on the posterior left, which places it outside the definitions of *Montfortia* and *Montfortista* as used here.

Distribution and Occurrence: Western Pacific, intertidal and shallow sublittoral zones.

Taxonomic History: Authors have generally regarded *Montfortista* as the same as *Montfortia*, but it is here distinguished from *Montfortia* in having a much more strongly projecting anterior rib.

Genus *Hemitoma* Swainson, 1840
(Figs. 10, 28)

Hemitoma Swainson, 1840. Type species (monotypy): *Patella tricostata* G. B. Sowerby I, 1823, *non* Gmelin, 1791 [= *Patella octoradiata* Gmelin, 1791] (Fig. 28). Caribbean. Other figure: Abbott, 1974: fig. 52.
Subemarginula Gray, 1847. Type species (monotypy): *Patella octoradiata* Gmelin, 1791.

Shell (Fig. 28, *octoradiata*): Selenizone lacking, shallow notch visible only in frontal view. Apex central, not recurved; eight strong primary ribs, with lesser secondary ribs between.

External Anatomy: The external morphology and the arrangement of the internal organs for *Hemitoma octoradiata* was illustrated by Odhner (1932: figs. 10, 11). The type species *octoradiata* is highly unusual for the Fissurellidae in having a narrow bright red edge to the foot and the mantle edge, which are green away from the edges.

Radula (Fig. 10, *octoradiata*): Rachidian and laterals with transverse ridge at middle position on shaft, upper region of shaft thicker than lower; overhanging edge not divided into finer cusps; pluricuspid with deep division, with two small cusps on outer edge; outer edge of pluricuspid articulating with lateromarginal plate.

Previous SEM figures of radula *H. octoradiata* – Hickman, 1981: fig. 7; Hickman, 1998: fig. K.

Other Examined Whole Mount Preparations: *H. octoradiata*, LACM 65-26.25.

Comparisons: This has the same number of primary ribs as in the new genus *Octomarginula*, but differs from that genus in not having the slit and selenizone. The shell differs from *Montfortia* and *Montfortista* in its eight ribs and non-projecting, non-recurved apex. The anterior view (Fig. 28) shows a notch that is less indented than that of *Montfortia* (Fig. 26) or *Montfortista* (Fig. 27).

Species: There are numerous synonyms for the type species cited by Turner (1959). A species from Mozambique determined by Herbert (1987: fig. 6) as *polygonalis* (A. Adams, 1852) agrees with *Hemitoma* in having the central apex and the count of primary ribs. The shell of the type species is always encrusted, as it lives exposed in intertidal zone.

Taxonomic History: This is the first named genus for the subfamily; it was used too broadly by Thiele (1917), and by subsequent authors. Most of Thiele's (1917) illustrations show species now assigned to other genera. Kilburn (1978: 478) keyed *Hemitoma* as having a selenizone forming a coarse ridge; such species with the selenizone are now assigned to *Montfortula* Iredale, 1915.

II. Radula with transverse ridge replaced by pustules, notch absent, with interior groove only

Genus *Montfortulana* Habe, 1961
(Figs. 11, 29)

Plagiorhytis Fischer (*non* Chaudoir, 1848), 1885. Type species (original designation): *Clypidina sulcifera* A. Adams, 1851. Locality unknown. Figure: Thiele, 1917: pl. 15, figs. 9, 10.
Montfortulana Habe, 1961. Type species (original designation): *Subemarginula* (*Plagiorhytis*) *eurythma* Dautzenberg, 1907. Lifou, Loyalty Islands. Figure: Thiele, 1917: pl. 14, figs. 10–12.

Shell (Fig. 29, species undetermined): Apex anterior of center, not recurved; radial ribs alternating with numerous primaries and smaller secondaries, anterior channel of inner surface deflected to right antero-lateral position, corresponding notch very weak.

Radula (Fig. 11, species undetermined): Transverse ridge condition obscured by dark lighting on shaft; cusps of rachidian and first three pairs of lateral teeth, deeply split on either side; fourth lateral narrow with narrow overhanging cusp; pluricuspid with broad, angular overhang, with one smaller cusp on outer side. Narrow lateromarginal plate between pluricuspid and inner marginals.

Comparisons: Differing from other hemitomine genera in having the notch and its interior groove running from the apex to the right antero-lateral corner. In having a reduced transverse ridge, the morphology of the rachidian and lateral teeth is most like that of *Clypidina*, differing in a narrower aspect of the tooth shafts.

Species: Two or three species, Indo-Pacific: *Clypidina sulcifera* A. Adams, 1851 ["hab. Unknown"]; *Subemarginula* (*Plagiorhytis*) *eurythma* Dautzenberg, 1907 [Lifou, Loyalty Islands]. The illustrated specimen from Tahiti (Fig. 29) is more elongate than the figures for the two species previously assigned, so it is likely to be an undescribed species.

Taxonomic History: The right anterior lateral position of the interior groove is well illustrated by Thiele (1917: pl. 15, fig. 10, *sulcifera* A. Adams, 1851, and pl. 14, fig. 12, *eurthyma* Dautzenberg, 1907), both of which were placed by Thiele in *Clypidina*. Christiaens (1991: 38) listed *Montfortulana* as a subgenus of *Clypidina*. Higo et al. (1999: 43) listed *Montfortulana* as a full genus of Emarginulinae. Unfortunately, Sasaki in Okutani, 2000, did not figure a Japanese species of *Montfortulana*.

Habe (1964: 4) provided an English translation of the original Japanese description: "The shell is roundly oval, conical, moderately elevated and rather solid. The apex is slightly anterior from the center. From the apex about 15 primary radial ribs run to the margin; there are sometimes secondary riblets between these main ribs. There is an internal groove running from the apex to the right antero-lateral corner, rather than to the anterior end as seen in the genus *Clypidina* Gray."

Genus *Clypidina* Gray, 1847
(Figs. 12, 30)

Clypidina Gray, 1847. Type species (monotypy): *Patella notata* Linnaeus, 1758 (Fig. 3) India and Sri Lanka. Other figure: Subba Rao, 2003: pl. 2, figs. 5, 6).

Shell (Fig. 28, *notata*): Large for subfamily, apex central, not recurved; radial ribs even, black at crests, short notch visible only in frontal view only in early juvenile shell, connecting to narrow anal groove leading to shell apex.

Radula (Fig. 11, *notata*): Rachidian and three pairs of laterals of similar size and morphology, with shaft broad at base; overhanging cusps deeply split; shafts of third pair of laterals with transverse thickening; fourth pair or laterals smaller; pluricuspid larger, with rounded main cusp and smaller side cusps. The radula of *Clypidina* is unlike other hemitomine genera (except for *Montfortulana*) in having the transverse ridge apparent only as a thickening with pustules on the third laterals.

Previous SEM figures of radula *Clypidina notata* – Hickman, 1980: fig. 6a.

External Anatomy: The anatomy of *Clypidina notata* was described and Illustrated by Odhner (1932: figs. 8, 9).

Comparisons: *Clypidina* is unique in not showing a notch in anterior view, although the shell interior has the channel that leads to the apex.

Species: The type species is known only from the Indian Ocean; LACM records are from Sri Lanka and Goa, India. It occurs in the exposed intertidal. This is probably a monotypic genus.

Taxonomic History: This genus has been used more broadly by early authors, including Thiele (1917: 126), particularly for a number of species later assigned to *Montfortula* Iredale, 1915, and *Montfortulana* Habe, 1961. As noted above, Christiaens (1973, 1991) incorrectly used *Montfortula* as a subgenus of *Clypidina*, contrary to the radula definition of Thiele, 1917, 1929).

DISCUSSION

Morphological Evidence in Support of Hemitominae

The hemitomine lineage of Fissurellidae is here diagnosed on shell and radular characters. The defining feature of the radula – the transverse ridge of the teeth of the central field – is a synapomorphy unknown in any other genera of fissurellids. The transverse ridge of the rachidian and laterals has previously been illustrated in the line drawings of Farfante (1947), Christiaens (1987), and Herbert (1987), but these drawings do not convey the three dimensional aspect revealed with SEM, that the upper part of the tooth is actually thickened at the juncture and projects to overlap the basal portion of the tooth. The transverse ridge has a derived state in the genera *Montfortulana* and *Clypidina*, in which it is expressed by projecting pustules.

On shell characters, the genera that retain the slit and selenizone in mature stages are regarded as the basal genera of Hemitominae, because an open slit and selenizone is plesiomorphic for *Emarginula*, which is the oldest known genus of Fissurellidae. The basal genera of Hemitominae differ from *Emarginula* in having a lower profile, a shorter slit, and more irregular primary and secondary radial ribs. The more derived genera of Hemitominae retain the groove, but have lost the slit and the selenizone, which has been replaced with a notch that shows in the anterior view of the shell, except for *Clypidina*, which lacks the notch.

The course of evolution of the two groups has differed. In the stem group Emarginulinae, the lineage with an open slit yields shell forms with the anterior margin closed, to enable the slit to become modified, first by becoming sealed at the margin as in *Rimula* Defrance, 1887, and enlarged as an excurrent foramen, in the process losing the selenizone in the mature shell, as in *Puncturella* Lowe, 1827. In the hemitomine lineage, the derived genera do not form excurrent holes in the shell; instead, the derived genera lose the selenizone in the mature stage, becoming more limpet-like, retaining only the small notch at anterior edge of the shell, which serves as the excurrent channel out of the mantle cavity.

It might be expected that the derived hemitomine genera would reduce the size of the paired ctenidia, considering that the direction of flow is reduced by the necessity for the current to exit the mantle cavity at the uppermost anterior edge of the shell, via the short slit or notch. However, the paired ctenidia illustrated by Odhner (1932), for type species of the genera *Clypidina* and *Hemitoma* are not smaller than those of other fissurellids. Both of these genera are in the derived group that lives exposed to wave energy in the intertidal, so it seems evident they are able to maintain the flow through the mantle cavity by living in a high energy environment.

Fossil Record of Hemitominae

The earliest occurrence of Hemitominae is here recognized in the genus *Loxotoma* Fischer, 1885, occurring from the Upper Jurassic to Eocene of Europe. The type species, *Loxotoma neocomiensis* (d'Orbigny, 1843), is a strikingly asymetrical species of the Neocomian Early Cretaceous of France, with a broad notch and selenizone on the right anterior-lateral margin, as figured by Knight et al. (1960: 228, fig. 141–7a, b). This genus agrees with my diagnosis of the subfamily in having a non-recurved central apex, with primary and secondary ribs alternating in strength, and a very short slit that is deflected to the right. The selenizone is broader than that of living genera, but it calls to mind the scooped short slit of the early stage of *Octomarginula* (Fig. 22).

Sohl (1992: 418, figs. 5.1–5.3) illustrated a specimen as "*Emarginula* sp.," from the Upper Cretaceous of Jamaica, which he left unnamed, because the low profile and lack of the posteriorly directed apex and broader selenizone than that of other Cretaceous species of *Emarginula* that he described in the same paper. The comparison was not made to *Loxotoma*, but it is now clear to me that Sohl's illustrated specimen is a *Loxotoma* with the slit not so deflected as in the figured type species of *Loxotoma*.

Sohl (1992) also noted that *Emarginula gabbi* Stewart (1927: 313, pl. 23, fig. 10), from the Campanian Late Cretaceous of California, "also has a depressed profile and strong radial sculpture, but the ribs are closer spaced and the selenizone is much narrower." Other species of similar profile are mentioned by Sohl (1992: 418). All of these species indicate that the basal forms of Hemitominae were broadly represented in the Mesozoic. The Mesozoic genera of Hemitominae are in need of further study, which is beyond the scope of this report.

Two of the living hemitomine genera have a fossil record in the Caribbean. These are the new genus ***Hemimarginula***, which has a fossil record in the Pliocene, as mentioned under that genus, and the genus *Montfortia* in the early Pliocene. Ladd (1966) illustrated a few species of hemitomine genera in his account of Cenozoic gastropods from island groups of the Western Pacific, nearly all of which were of Holocene age; he cited the then available literature by region.

Recurring Asymmetry of Hemitomine Genera

A rightward shift in the position of the selenizone is a recurring theme in the Jurassic to Cretaceous genus *Loxotoma*, one undetermined living species of *Montfortula* illustrated here (Fig. 25), and the living genus *Montfortulana* (Fig. 29). There are less pronounced indications of asymmetry in *Octomarginula natlandi* (Figs. 21, 22), *Montfortia emarginata* (Fig. 26), *Montfortista panhi* (Fig. 27), and *Hemitoma octoradiata* (Fig. 28). Similar patterns of asymmetry are unknown in living species of Emarginulinae and Fissurellinae.

Shell and Radula Evolution of Subfamily Fissurellinae

All genera of the subfamily Fissurellinae have an apical foramen and are therefore not derived from the stem genus *Emarginula*, but must be derived from a foramen-bearing group. The candidate group would be unlike *Diodora*, not having a truncate callus bordering the inner edge of the foramen, and also lacking the hooks of the shell muscle and muscle scar, as in the derived emarginuline genera *Lucapina* Pilsbry, 1890, and *Stromboli* Berry, 1954. The dominant shell sculpture would be radial, rather than the sharply clathrate and concentric sculpture of emarginuline and hemitomine genera. The derived emarginuline genus *Lucapinella* Pilsbry, 1890, has radial sculpture like that of *Fissurella*, and would be the logical connecting genus, if it had a fossil record.

The fissurelline radula is diagnosed as having an extremely narrow rachidian (McLean, 1984c). The rhomboidal rachidian of large-shelled species in the *Fissurellidea* group illustrated by McLean (1984b) is much broader than that of Fissurellinae, because it serves to separate the paired, large pluricuspid teeth positioned between the lateral and marginal teeth. However, within the Emarginulinae, narrow and elongate teeth of the central teeth are known in many of the small-shelled, deep-water genera of the *Fissurisepta* shell form reviewed by McLean & Geiger (1992: figs. 2G, 3G, 3L, 6G, 7D, 10G), which suggests that an understanding of transitional taxa between derived emarginulines and fissurellines should be sought in specimens that are small-shelled at maturity or small in juvenile stages. This may well show that distinctions between the subfamilies Emarginulinae, Hemitominae, and Fissurellinae are blurred during early ontogeny. There is a striking similarity between the mature radula of *Profundisepta profunda* (Jeffries, 1876) shown by McLean & Geiger (1998: fig. 3G) and the mature hemitomine radula illustrated here, because the narrow outer laterals of that species show a mid-shaft heel that calls to mind the transverse ridge of the hemitomine radula.

First Appearance of Fissurellid Subfamilies

Mazaev (1998) described a Paleozoic genus *Retchitsella* from the Upper Carboniferous of the Moscow Basin, based on a species of small size (2.2 mm) having clathrate sculpture and a high profile. He assigned *Retchitsella* to Emarginulinae, although there is neither a slit nor a selenizone. In the absence of these most diagnostic features of Fissurelloidea, that assignment has to be provisional.

Based on Warén & Bouchet (2005) and Knight et al. (1960), the earliest appearance of Fissurellidae Fleming, 1822, is Middle Triassic for *Emarginula* Lamarck, 1801, for the subfamily Emarginulinae Children, 1834. Sohl (1992) showed that *Diodora* was flourishing during the Late Cretaceous of the Caribbean; he also claimed that *Fissurella* was present because his species "*Fissurella*" *kollmanni* lacks the truncate interior callus ring of *Diodora*. However, because that species has clathrate sculpture like that of *Diodora*, I instead consider it evidence for a genus with an oval callus ring, comparable to *Stromboli*, a member of a generic group of derived emarginulines indicative of the transitional source group leading to fissurellines.

As detailed above, the Hemitominae Kuroda, Habe, & Oyama, 1971, are traced to *Loxotoma* Fischer, 1885, with a first appearance in the Upper Jurassic of Europe (Knight et al., 1960).

With the above mentioned correction of Sohl's Cretaceous record, the earliest member of the subfamily Fissurellinae Fleming, 1822, is still *Atractotrema* Cossmann, 1888, of the European Eocene (as in Knight et al. 1960). The better known genus *Fissurella* Bruguière, 1789, arose and radiated during the Oligocene of Europe.

The Molecular Phylogeny of Aktipis et al. (2011)

The recently published "five-gene molecular phylogeny" of selected genera of Fissurellidae by Aktipis et al. (2011) sequenced only five of the species here assigned to four different genera of the nine genera assigned to Hemitominae in my morphological analysis. Assigned to their concept of Hemitominae were *Hemitoma octoradiata* (type species of *Hemitoma*), and "*Hemitoma panhi*" (here assigned to *Montfortista*). Genera used by me for these species are considered to be in the derived group of hemitomine genera because the slit and selenizone are present only in the early juvenile stage. Species here treated as Hemitomine, but assigned to Emarginulinae by Aktipis et al. (2011) were *Emarginula variegata* and *E. foveolata fujitai* (both here assigned to new genus ***Variegemarginula***) and *Montfortula rugosa* (type species of *Montfortula*).

Genera recognized by me for these three species are considered basal in my definition of Hemitominae because they retain the slit and selenizone at all sizes. As could be expected, the first two species emerged as a sister group on their "maximum likelihood tree" (Aptikis et al., 2011: fig. 3) and the second three species formed another branch on the same tree. However, the first pair of their examined species emerged as sister to their only examined species of *Puncturella* and *Cranopsis* (genera regarded by McLean & Geiger, 1990 as within the emarginuline lineage). The second three species emerged on their Figure 3 between their species of true *Emarginula* and such other emarginuline genera as *Emarginella*, *Scutus*, and *Tugali*. This is a discrepancy in need of comment and possible explanation.

First, the observation that the length of the "*Hemitoma*" branch in the "maximum likelihood tree" (Fig. 3, of Aptikis et al., 2011) far exceeds the length of all other branches, which suggests the need for the inclusion of additional taxa of the genera regarded as derived in my morphological analysis.

A close look at tree B (Fig. 2B of Aptikis et al., 2011), the "strict consensus of all trees," indicates an unresolved polytomy of 16 branches, including 8 outgroups, all of which are subordinate to the pleurotomarioid outgroup. On this tree, my genera of Hemitominae appear twice, first, at the top, with the sister group *Hemitoma octoradiata/ Montfortista panhi* (regarded by me as derived hemitomines) preceding the rest of the outgroups, and again only as sister to *Puncturella/Cranopsis* standing alone in their analysis, preceding all the other species of Emarginulinae on their tree B. The last grouped emarginulines of their tree B are the type species of *Montfortula* and V*ariegemarginula*, which are placed by me among the basal genera in my reinstated Hemitominae.

The improbability of connecting these two groups was noted by Aptikis et al. (2011: 250): "… the outer lateral radula and pluricuspid teeth differ between the genera, and *Hemitoma* lacks a visible shell fissure while *Puncturella* and *Cranopsis* have a fissure on the anterior slope. Furthermore, *Hemitoma* are generally found in a range of ocean depths from shallow water to 200 m, while *Puncturella* and *Cranopsis* are mainly deepwater organisms. Recovery of *Hemitoma* sister to *Puncturella* + *Cranopsis* was therefore an unexpected result of this analysis and warrants further investigation with increased species sampling from both genera. Nevertheless, results of this study suggest that a clade comprised of *Hemitoma*, *Puncturella* and *Cranopsis* could constitute a fourth subfamily of fissurellids, recognized here as Hemitominae Kuroda et al., 1971."

One correction to the above is that the redefined genus *Hemitoma* and other related genera occur in the intertidal and shallow sublittoral zones, chiefly in the tropics. It is more exacting to note that *Puncturella* and *Cranopsis* occur under cold conditions, submergent in deep water at tropical latitudes and in shallower water at higher latitudes.

I agree that their results do indeed need further investigation with increased sampling, but a connection of *Hemitoma* to *Puncturella* and *Cranopsis* can only be dismissed as highly unlikely. The polytomy indicated in their Figure 2B indicates that their molecular analysis is defective, so their definition of Hemitominae is rejected here.

The next molecular analysis should include the genera *Clypidina* and *Montfortulana*, which have what I am considering to be a derived state of the radula in my definition of Hemitominae.

Feeding Ecology

Hemitomine genera of the rocky intertidal (*Hemitoma*, *Clypidina*, *Montfortula*, *Montfortulana*) are easily mistaken for patellid or siphonariid limpets because the notch does not show in dorsal view. One hemitomine species (*Montfortula rugosa*) is known to feed on algae in the rocky intertidal of southern Australia (Creese, 1978), as mentioned in more detail under that genus. I have not found citations that treat the feeding in *Hemitoma* and *Clypidina*, but expect that similar feeding would be the case because of the close similarities in radular structure and because these genera also live in the exposed intertidal zone in which algal mats would be the obvious food source.

Feeding in the hemitomine genera is also is comparable to the feeding of *Fissurella* species of the subfamily Fissurellinae, in which algal feeding is known (Ward, 1966; Bretos, 1978; McLean, 1984c; Franz, 1990a, b).

Most genera of emarginuline fissurellids are more cryptic in offshore habitats and feed upon sponges or other sessile invertebrates. However, two of the basal hemitomine genera (***Hemimarginula*** n. gen., ***Variegemarginula*** n. gen.) occur in unexposed habitats in the rocky intertidal and at shallow depths.

ACKNOWLEDGMENTS

My SEM views of the radulae were made in the 1990s at the University of Southern California by the late Clif Coney, former collection manager of the LACM mollusk collection. I thank Daniel L. Geiger of the Santa Barbara Museum of Natural History for providing the images of the radula for *Montfortulana* sp. Figures from my radula SEMs and my photos of shells were prepared in Photoshop by Brian Koehler, scientific illustrator (LACM). Gary Rosenberg of the Academy of Natural Sciences, Philadelphia, confirmed that type specimens for the two Caribbean species of Heilprin had been switched. Gonzalo Giribet of Harvard University kindly provided the prepublication PDF of Aptikis, et al. (2011). I thank Daniel L. Geiger for many helpful suggestions, which improved the manuscript, particularly the advice regarding the published work of Aptikis et al. (2011) on molecular phylogeny. The manuscript was commented upon by anonymous reviewers, who made valuable suggestions. Lindsey T. Groves (LACM) read the manuscript and noted corrections. I particularly thank Douglas J. Eernisse of California State University at Fullerton for a detailed review and helpful suggestions.

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Revised ms. accepted 1 July 2011

RESEARCH NOTE

MALACOLOGIA, 2011, 54(1–2): 431–435

THE GENUS *SPHENIA* TURTON, 1822 (BIVALVIA: MYIDAE) FROM SHALLOW WATERS OF ARGENTINA

Guido Pastorino* & Maria Bagur

Museo Argentino de Ciencias Naturales, Av. Angel Gallardo 470 3° piso lab. 80 C1405DJR, Buenos Aires, Argentina

INTRODUCTION

The genus *Sphenia* was first reported in southern South America by Pilsbry (1899), who described *Sphenia hatcheri* from shallow Patagonian waters. Later, Castellanos (1965) published a short note with comments on the type material of this species, studied by the late J. J. Parodiz at the Academy of Natural Sciences of Philadelphia, USA. Finally, in her catalogue of marine mollusks from Buenos Aires province (1970: 279), Castellanos mentioned Mar del Plata (38°S) as the farthest north distribution of this species. Coan (1999) published a detailed review of the Pacific species of *Sphenia*, including some interesting data about two Atlantic species, *S. hatcheri* and *S. fragilis*. Scarabino & Zaffaroni (2004) and Scarabino et al. (2006) briefly reported and discussed the distribution of these species in Uruguayan waters.

After an exhaustive study of the intertidal endolithic fauna of bivalves from Buenos Aires province, Argentina, new findings of specimens of *Sphenia* allow the reillustration and comparison of these species. In addition, new distributional ranges are provided.

MATERIAL AND METHODS

Specimens collected from the intertidal sedimentary rock shoal, close to Santa Elena, Buenos Aires province, Argentina (37°51'8.81"S, 57°30'21.65"W), were the core of material studied. Additionally, all the specimens housed at the collections of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires (MACN), and Museo de La Plata, Argentina (MLP) were studied. Scanning electron microscope images were produced with a Philips XL30 at the MACN. Most photographs were taken using a digital camera. All images were digitally processed with the appropriate software.

SYSTEMATICS

Sphenia fragilis
(H. Adams & A. Adams, 1854)
Figures 1–8

Synonyms: (complete list in Coan, 1999)

Tyleria fragilis H. Adams & A. Adams, 1854: 418.

Sphenia hatcheri. Castellanos, 1970: 279 (*non* Pilsbry, 1899, *partim*); Figueiras & Sicardi, 1970: 22, pl. 7, fig. 103 (*non* Pilsbry, 1899).

Corbula iheringiana Pilsbry, 1897: 295, pl. 7, figs. 24–26; Castellanos 1970: 270.

Sphenia fragilis. Coan, 1999: 105, figs. 2–6, 18, 24; Scarabino et al., 2006: 161; Mikkelsen & Bieler, 2008: 378, fig.

Material Examined: (sp. = complete specimens, otherwise specified). 37°51'8.81"S, 57°30'21.65"W, Santa Elena, Buenos Aires, 16 sp., intertidal (MACN-In 38283); Mar del Plata, Buenos Aires, 1 sp. (MACN-In 10757); Miramar, 1 sp. (MACN 8451-15); Miramar, 2 sp. (MACN-In 8451); Miramar, Buenos Aires, 1 sp. (MACN-In 29511); Miramar, 1 left valve (MLP 2365-2); Río Quequén, Buenos Aires, 3 sp. (MACN-In 29514); Puerto Quequén, 1 sp. (MACN-In 19552); 41°12'S–62°54'W, 1 sp., 1 left valve, in 27.4 m depth (MACN-In 20652); Puerto Militar, Buenos Aires, in 30 m depth, 2 sp. (MACN-In 11142).

Remarks: The specimens studied showed a considerable variation in shell shape because of the constraints imposed by their nestling habit and consequent dependence on the substrata where the animal grows. Figures 1–5 illustrate specimens in which the height and length of, right and left valves, are the most variable feature. The chondrophore, as it was pointed out by Coan (1999), holds the main difference between *S. fragilis* and *S. hatcheri*. As it can be seen in Figure 19, the posterior

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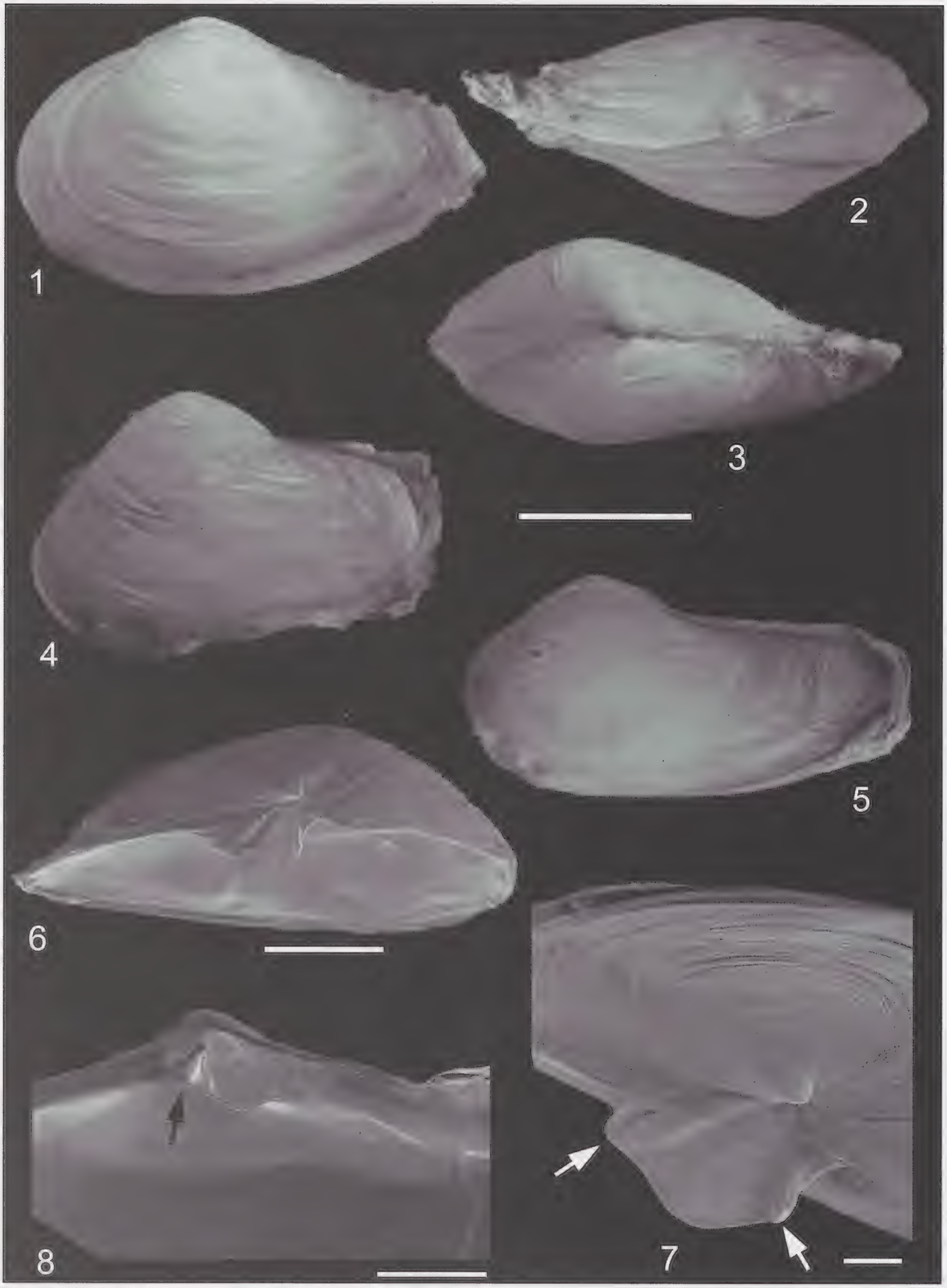
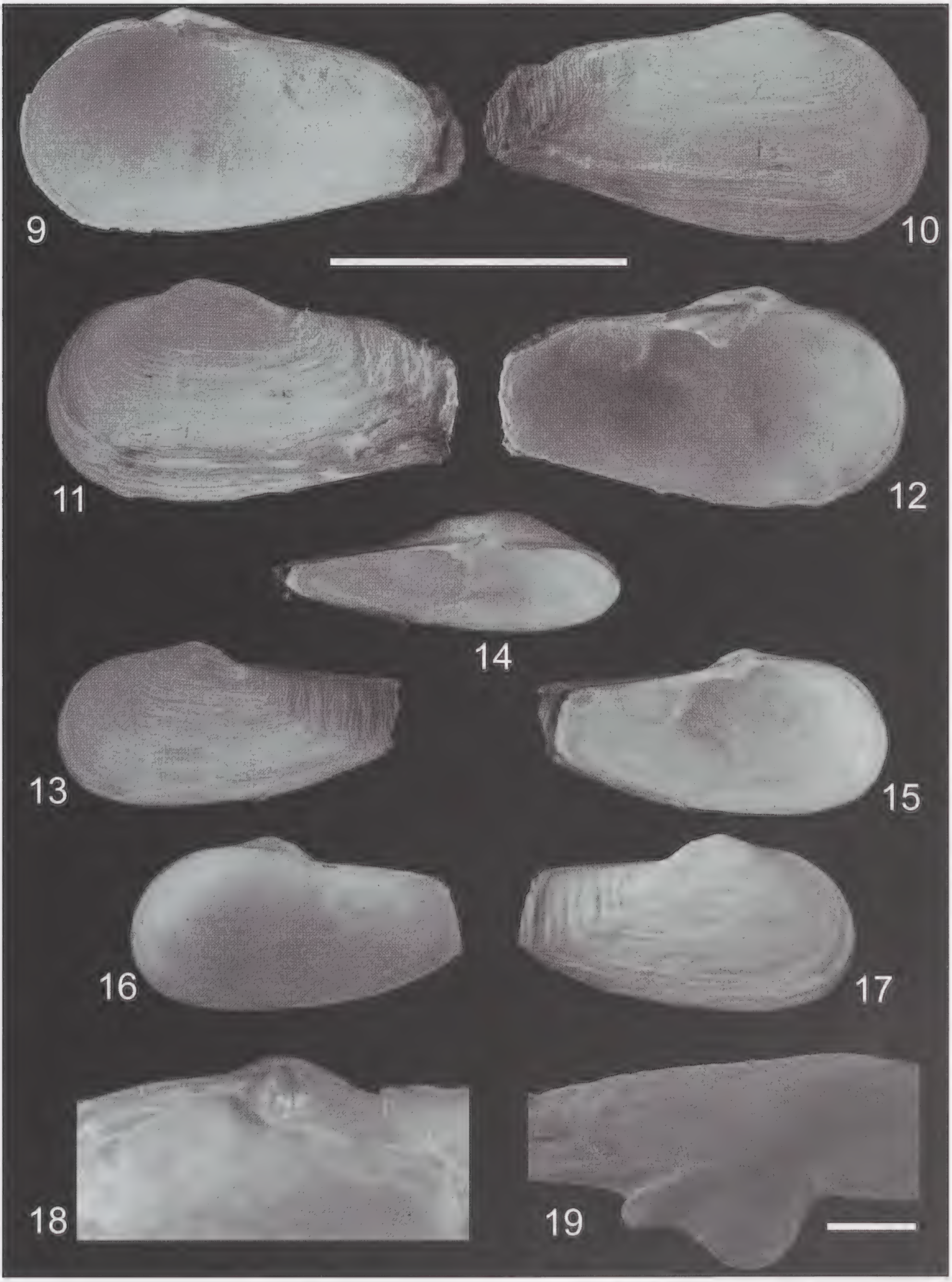
*Corresponding author: gpastorino@macn.gov.ar



FIGS. 1–8. *Sphenia fragilis* (H. Adams & A. Adams). FIG. 1: Left valve; FIG. 2: Ventral view of the same specimen in 1; FIG. 3: Dorsal view of the same specimen in 1; FIG. 4: Left valve; FIG. 5: Left valve; FIG. 6: Inner view of left valve, tilted to show the chondrophore. Scale bar Figs. 1–5 = 3 mm; FIG. 7: SEM image of the left valve, right arrow showing a ridge on the anterior margin of chondrophore, left arrow showing the posterior ridge of condrophore slightly projected. Scale bar = 200 µm; FIG. 8: SEM image of right valve showing the hinge area, arrow pointing the anterior cardinal teeth. Scale bar = 500 µm. All specimens from MACN-In 38283.



FIGS. 9–19. *Sphenia hatcheri* Pilsbry. FIG. 9: Inner view of right valve; FIG. 10: Outer view of the same in 9; FIG. 11: Outer view of right valve; FIG. 12: Inner view of the same in 11; FIG. 13: Outer view of right valve; FIG. 14: Left valve slighly tilted to see the hinge area; FIG. 15: Inner view of the same in 13; FIG. 16: Inner view of right valve; FIG. 17: Outer view of the same in 16. Scale bar for all specimens = 1 cm; FIG. 18: Detail of the hinge of right valve; FIG. 19: SEM image of the chondrophore. Scale bar = 500 µm. All specimens from MACN-In 37986.

ridge of the condrophore of *S. hatcheri* in the left valve is longer and clearly projecting out of the ventral edge, whereas in *S. fragilis* this ridge is weakly or not projecting (Fig. 7). In addition, *S. fragilis* has a distinctive ridge on the anterior margin of the condrophore (Fig. 7, right arrow). A larger anterior cardinal tooth in the right valve of *S. hatcheri* is another distinguishing feature. The same tooth is also present in the right valve of *S. fragilis* but much smaller and anterior to a deeply recessed resilifer (Fig. 8, arrow). Also *S. hatcheri* is larger than *S. fragilis* (30.1 mm vs. 12.7 mm according to Coan, 1999).

Coan (1999) cited *S. fragilis* as occurring in both eastern Pacific and western Atlantic oceans. We have studied material from Uruguay and Argentina. The distribution range in both countries covers the entire marine coast from Uruguay to 41°12'S–62°54'W in Argentina. Most of the material comes from the intertidal zone with the exception of two lots collected at about 30 m depth.

Sphenia fragilis is found usually intertidally among and under the talus of the Rhodophyta *Corallina officinalis*. Also, sometimes it is part of the fauna associated to the byssal filaments of *Brachidontes rodriguezii*, the most abundant mytilid forming large banks at the study area. Living together with *S. fragilis* is *Hiatella meridionalis*, another byssate bivalve fairly common in this habitat; they share the same crevices, a usual behavior already reported by Yonge (1951) for *Sphenia binghami* and *Hiatella* sp. from Port Erin, Isle of Man, United Kingdom.

Coan (1999) pointed out the wide distribution of *S. fragilis*. This distribution is apparently not only Recent, as Scarabino & Zaffaroni (2004) confirmed its presence of *S. fragilis* in Quaternary deposits of Uruguay.

Sphenia hatcheri
Pilsbry, 1899
Figures 9–19

Synonymy: (complete list in Coan, 1999)
Sphenia hatcheri Pilsbry, 1899: 128, pl. 1, fig. 5, 6; Carcelles, 1950: 82, pl. 5, fig. 94; Carcelles & Williamson, 1951: 347; Castellanos, 1965: 173–175, pl. 1, figs. 1–8; Castellanos, 1970: 278–279, pl. 25, figs. 9–11 (*partim*); Scarabino & Zaffaroni 2004: 11.
Sphenia subequalis Dall, 1908: 422–423; Carcelles, 1950: 82.

Material Examined: Puerto Deseado, 1 sp. (MACN-In 17753); 4 km S of Punta Desengaño, San Julián, Santa Cruz, several valves (MACN-In 36931); 7.5 km S of San Julián, 1 sp. (MACN-In 36919); intertidal coast near of Estancia La Costa, Coyle, Santa Cruz (MACN-In 37986); Santa Cruz coast between Coyle and Río Gallegos, 3 sp. (MACN 10125); Santa Cruz, (MACN-In 29513); Cabo Buen Tiempo, Santa Cruz, several sp. (MLP 10246); Monte Tigre, S coast, Río Gallegos, Santa Cruz, 5 left, 1 right valves (MLP 1681); Monte Tigre, Río Gallegos, Santa Cruz, 1 sp., 4 left, 2 right valves (MLP 1349); Monte Tigre, Río Gallegos, Santa Cruz, (MLP 2041); San Sebastián, Tierra del Fuego, 8 sp., 11 left, 9 right valves; (MACN-In 12617); Punta María, Rio Grande, Tierra del Fuego, 7 sp. (MACN-In 37910); Río del Fuego, Tierra del Fuego, several sp. (MACN-In 12616); 54°53'S, 68°14'W, Bridges Is., Tierra del Fuego, 1 left, 1 right valves (MLP 12225).

Remarks: According to Coan (1999), based on Figueiras & Sicardi (1970) and Castellanos (1970), the distribution in the southwestern Atlantic is from La Paloma (34°40'S) in Uruguay to Mar del Plata, in Argentina. Coan (1999) suggested that these northern records may represent sporadic recruitment. Along the Pacific coast of South America, *S. hatcheri* occurs from Tierra del Fuego to Isla Chiloe in Chile. We restricted here the distribution on the southwestern Atlantic from Tierra del Fuego to Puerto Madryn, Golfo Nuevo, Chubut, Argentina, the latter based on specimens in the ANSP 170466, reported by Castellanos (1965). No specimens of *S. hatcheri* either from Uruguayan or Buenos Aires province coasts have been found during our field work nor in the collections examined. Those records north of Puerto Madryn cited by Coan (1999) from the published literature are here considered as belonging to *S. fragilis*, as well as specimens from Mar del Plata, Buenos Aires province (MACN-In 10757) mentioned by Castellanos (1970) and repeated by Coan (1999).

ACKNOWLEDGEMENTS

E. V. Coan (Palo Alto, California, USA) and F. Scarabino (MNHNM, Montevideo, Uruguay) made very useful comments that improved an early version of the manuscript. L. P. Arribas kindly helped during field work. We are grateful to A. Tablado (MACN-In Buenos Aires, Argentina) and C. Damborenea (MLP) for access to collections under their care. This work benefits with the criticism of two anonymous reviewers. It was partially supported by the projects PICT 942 from the National Agency for Scientific and Technical Promotion, Argentina, and PIP 0732 from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). We acknowledge funding by CONICET of Argentina, to which GP belong as a member of the research carrier and MB as fellow.

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Revised ms. accepted 10 May 2011

OBITUARY

MALACOLOGIA, 2011, 54(1–2): 439–440

IN MEMORIAM:
DR. J. FRANCES ALLEN, APRIL 14, 1916–FEBRUARY 11, 2011*

Dr. J. Frances Allen, 1944 (Photograph courtesy of Lockie Jo Allen)

Dr. J. Frances Allen, ca. 1980 (Photograph courtesy of Lockie Jo Allen)

Dr. J. Frances Allen, a biologist with broad training and experience, including malacology, was a longtime friend of *Malacologia* and the Institute of Malacology, and served as advisor in the early days before the journal was formally established, and continued her interest and support of the journal throughout the rest of her life. She referred to the Sponsor Members of the Institute of Malacology as “my boys,” and was proud of their accomplishments.

Dr. Allen was born in Arkville, New York, the daughter of J. W. Allen and Mattie Jo Linkous Allen. She attended schools in Owego and Roxbury, New York, graduating from Roxbury Central High School in 1934. Dr. Allen attended Radford State Teachers College (now Radford University), Radford, Virginia, receiving her Bachelor of Science degree in 1938. During the summer of 1937 she received training at the Chesapeake Biological Laboratory, Solomons Island, Maryland, and during the summer of 1938 she took courses at the University of Virginia’s Mountain Lake Biological Station. During the years 1938–1946, J. Frances Allen taught secondary school science in Virginia, West Virginia and New York State, and during the summers of 1942, 1944 and 1945 she was Assistant Professor of Science at Radford State Teachers College. While teaching in Virginia, Dr. Allen was one of the founders of the Virginia Junior Academy of Science and became its first Secretary. She was Biological Examiner for the New York State Department of Education during the summer of 1946. In the fall of 1946, she entered the University of Maryland’s graduate school, receiving the Master of Science

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*Modified from the *Northern Virginia Daily*, February 16, 2011 degree in 1948, and the Doctor of Philosophy degree in 1952. At the University of Maryland, J. Frances Allen was a graduate assistant during the years 1947–1948, instructor 1948–1952, Assistant Professor of Zoology and member of the graduate faculty 1952–1958.

In 1958, Dr. Allen joined the National Science Foundation (NSF) in Washington, D.C., as Associate Program Director of the Systematic Biology Program. In 1967 She left the National Science Foundation to become Chief of the Water Quality Requirements Branch, Office of Research and Development, Federal Water Pollution Control Administration (later named the Federal Water Quality Administration, and, subsequently the U.S. Environmental Protection Agency [EPA]). Among her many contributions while at EPA, Dr. Allen initiated the Biota of Freshwater Ecosystems Identification Manuals, which provided for freshwater biologists means to identify the myriad aquatic organisms in the country's freshwaters. At the time of her retirement in 1982, Dr. Allen was Staff Scientist-Ecology for the Science Advisory Board, Office of the Administrator, EPA. Among the awards she received were the Sustained Superior Performance Award from the National Science Foundation, and a Bronze Medal from the Environmental Protection Agency.

Dr. Allen was the United States Representative to the Organisation for Economic Co-operation and Development (OECD) World Conference on Water Quality in Paris, France, in 1973. In 1974, she attended the first International Congress on Ecology at The Hague, in the Netherlands.

In addition to her membership in various scientific organizations, Dr. Allen was a Fellow of the American Association for the Advancement of Science, Fellow of the Washington Academy of Sciences, Co-Sponsor *Emerita* of the Institute of Malacology, a trustee and member of the Executive Committee of the Sport Fishery Research Foundation, and she was one of the first Certified Fisheries Scientists. For nine years, Dr. Allen was editor of the American Fisheries Society retiree's newsletter, *Homopiscis rusticus*.

Among scholastic honor societies, Dr. Allen was elected Kappa Delta Pi (International Honor Society in Education), Pi Gamma Mu (International Honor Society in Social Sciences), Chi Beta Phi (National Honor Society to Support Collegiate Women), Sigma Xi (The Scientific Research Society), and Sigma Delta Epsilon (Graduate Women in Science).

In 1987, Dr. Allen was honored by the American Fisheries Society by the establishment and endowment of the J. Frances Allen Scholarship. This scholarship for $2500 is awarded annually to a female doctoral candidate whose emphasis is in the field of fisheries science. The intent of the scholarship is to encourage women to become fisheries professionals.

The Institute of Malacology is in the process of establishing a student scholarship fund specifically for the field of malacology.

Dr. Allen retired to upstate New York and died near Oneonta, N.Y.

John B. Burch

MALACOLOGIA, 2011, 54(1–2): 441–479

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Vol. 47, No. 1–2	20 July 2005
Vol. 48, No. 1–2	16 Feb. 2006
Vol. 49, No. 1	10 Nov. 2006
Vol. 49, No. 2	27 July 2007
Vol. 50, No. 1–2	9 June 2008
Vol. 51, No. 1	19 Mar. 2009
Vol. 51, No. 2	26 Aug. 2009
Vol. 52, No. 1	27 Jan. 2010
Vol. 52, No. 2	7 May 2010
Vol. 53, No. 1	19 Oct. 2010
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